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UNIVERSITY OF ALBERTA

Permineralized monocotyledons from the Middle Eocene Princeton chert locality, British Columbia, Canada

BY

© Diane Marie Erwin

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS OF THE

DEGREE OF

Doctor of Philosophy

IN

Paleobotany

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING, 1991

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Sincerely,

Ruth A Stockey

Ruth A. Stockey

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Permineralized monocotyledons from the Middle Eocene Princeton chert locality, British Columbia, Canada

SUBMITTED BY: Diane Marie Erwin

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IN

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Abstract

A diverse assemblage of exquisitely preserved monocotyledonous vegetative remains has been recovered from the Middle Eocene Princeton chert in southern British Columbia, Canada. Among these remains, four new taxa are described. A small petiole, Heleophyton helobioides Erwin et Stockey, displays aerenchymatous ground tissue and minute bundles arranged in five distinct series. This pattern is similar to that in petioles of the extant genus Echinodorus (Alismataceae), but Heleophyton differs in possessing bundle morphology like Butomus (Butomaceae). Rhizomatous palm stems with attached petioles and roots are described as Uhlia allenbyensis Erwin et Stockey. Petiole, midrib, and lamina structure places the fossil palm in the subfamily Coryphoideae where it shares several morphological and anatomical features with three genera: Rhapidophyllum, Brahea, and Serenoa. Two distinct plants represented by small herbaceous stems are described and named based on differences in ground tissue differentiation, bundle morphology, vessel characters, and root anatomy. Ethela sargantiana Erwin et Stockey are short rhizomes, up to 1.5 cm wide, with numerous adventitious roots, several cycles of sheathing leaves, and small lateral branches, 2-3 mm wide. Vessels with scalariform perforation plates are found in roots and leaves. Regions within the inner cortex and central cylinder are suggestive of a primary thickening meristem (PTM). In monocotyledons, a PTM is common among bulbs and rhizomes of the Liliidae, almost exclusively found in the Liliales and Asparagales. However, leaf anatomy and the occurrence of specialized vessels suggests a closer relationship to the orders Cyperales and Juncales. Soleredera rhizomorpha Erwin et Stockey are short, branched rhizomes up to 1.3 cm wide with attached roots and associated aerial stems. Vessels show simple perforation plates and are restricted to the roots. These fossils most closely resemble plants in the Liliales. The Middle Eocene Princeton monocotyledons represent the oldest and most completely known anatomically-preserved monocots reported from North America. Their discovery adds significantly to our knowledge of the vegetative morphology, anatomy, and diversity of Liliopsida in the early Tertiary of western North America.

Acknowledgements

This work was supported in part by NSERC (Natural Sciences and Engineering Research Council of Canada) grant A6908 to Dr. Ruth A. Stockey. Thanks are given to Dr. Ruth Stockey for her guidance, encouragement, and personal and financial support throughout the course of this study. Thanks are also extended to Dr. David D. Cass, University of Alberta, Edmonton, Alberta, for use of his laboratory facilities; Dr. Randall J. Bayer, Curator of the University of Alberta Vascular Plant Herbarium, for providing extant specimens of Echinodorus; Dr. James C. French, Rutgers University, for providing his unpublished manuscript on the vegetative anatomy of the Araceae and comments regarding the fossils; Dr. Larry H. Klotz, Shippensburg University, Shippensburg, Pennsylvania, for critical review of an earlier manuscript version of Chapter 5; Dr. Kathleen B. Pigg, Arizona State University, Tempe, Arizona, for lending an ear; Dr. P.B. Tomlinson, Harvard University, Petersham, Massachusetts, for helpful comments regarding fossil palm specimens; Dr. Natalie W. Uhl, Professor Emeritus, Cornell University, Ithaca, New York, for serving as external examiner and Charles Hubbard, Curator of Palms, Fairchild Tropical Gardens, Miami, Florida for supplying material of Rhapidophyllum hystrix and Serenoa repens; Ron Harris, the palm gardener at Huntington Gardens and Library, San Marino, California, for procuring specimens of Brahea and Washingtonia; and George Braybrook, University of Alberta, Edmonton, Alberta, for assistance with the SEM.

Special thanks are given to Rhonda L. Bear, her mother Enid, Don, Suzanne, Rerun, and Riggley for caring and providing a home away from home. My deepest thanks are given to Helen Ko whose devote friendship made the completion of this thesis possible.

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Chapter 1: Introduction

Our knowledge of the vegetation of western North America during the early Tertiary is based largely on compression/impression floras (e.g., Berry, 1926; Hollick, 1936; Bell, 1949; Arnold, 1955; MacGinitie, 1969, 1974; Wolfe, 1977; Wolfe & Wehr, 1987) and palynological studies (e.g., Rouse, 1962; Hills, 1965b; Boneham, 1968; Rouse et al., 1971; Mathews & Rouse, 1984). The published descriptions of most floras usually provide a detailed account of the dicotyledons present, but monocotyledonous remains are often excluded or only given brief mention (Daghlian, 1981; Wolfe & Wehr, 1987). In part, this is due to the lack of diagnostic features exhibited by monocot vegetative organs that are necessary to identify or relate a specimen to an extant family or even a superfamilial rank (e.g., micromorphology of leaf cuticle and epidermis, venation patterns, leaf shape and margin morphology).

In early studies of permineralized Tertiary plants from western North America, Arnold (1944, 1952) noted the potential for the study of anatomy and the importance of internal structure in revealing systematic affinities of isolated plant fossils which are not always apparent based on evidence from external morphology. Unfortunately, with the exception of isolated occurrences of Tertiary silicified plant remains in North America, Europe, and Asia (e.g., Reid & Chandler, 1933; Arnold, 1944, 1952; Chitaley, 1964; Miller, 1969, 1970; Tidwell et al., 1971, 1972, 1973; Ting, 1972; Ting & Harr, 1976; Collinson & Ribbins, 1977; Ribbins & Collinson, 1978; Thomasson, 1980a, b, 1984; Collinson, 1983; Stockey, 1983; Friis, 1985; Manchester, 1987; Tidwell & Parker, 1987, 1990; Tidwell & Jones, 1987; Tidwell & Nambudiri, 1989), sites yielding permineralized plants are rare (Basinger &

Rothwell, 1977). Among the most productive localities presently known are the Eocene Clarno chert in Oregon, the Deccan Intertrappean Series in India, and the Middle Eocene Princeton chert in southern British Columbia.

Diversity of the Clarno chert is relatively low compared to the floras of the Deccan Traps and Princeton chert. This low diversity may reflect the limited amount of study given to these plant fossils (Arnold & Daugherty, 1963, 1964) rather than their absence. However, the Clarno fossiliferous chert is not extensive and is only about 60 cm thick (Arnold & Daugherty, 1963). A lava sheet lies above the chert and in some places the underlying ash deposits are 135 m thick and contain abundant silicified wood (Arnold & Daugherty, 1963). The plants described from Clarno are largely pteridophytes and gymnosperms. These include two species of *Osmundites* (Arnold 1944, 1952), *Acrostichum preaureum* (Arnold & Daugherty, 1963), *Dennstaedtiopsis aerenchymata* (Arnold & Daugherty, 1964), *Equisetum* (Arnold, 1952; Dennis, 1974; Brown, 1975), and *Ginkgo*, plus unidentified twigs of herbaceous and woody dicotyledons, pollen, and spores (Arnold & Daugherty, 1963). A more diverse flora of fungi, algae, mosses, ferns, conifers, dicotyledons, and monocotyledons is found in the Deccan Intertrappean Beds and the Princeton chert.

The Deccan Traps are divided into the Lower, Middle, and Upper Intertrappean Series (Rao, 1936). The Lower and Upper Traps consist of sedimentary layers (Intertrappeans) sandwiched between consecutive lava flows (Traps). The Lower Traps are considered to be Eocene (Lakhanpal, 1970a, b) or Paleocene (McElhinny & Wellman, 1969), whereas the Upper

Traps are considered to be Miocene (Rao, 1936). The recent discovery of dinosaur egg shell fragments in the Intertrappean beds of Mohgaon Kalan, however, suggests some are of Maastrichtian age (Sahni et al., 1984) and not Eocene as previously thought based on the flora (Sahni, 1934).

Like the Princeton chert, the flora at Mohgaon Kalan is diverse and includes an assemblage of algae, mosses, heterosporous ferns, conifers, dicotyledons, and monocotyledons (Basinger, 1976a). Although the types of plants from Mohgaon Kalan are different from those in the Princeton chert, the quality of preservation is often comparable and both represent deposits of a fresh water ecosystem, possibly a lake or marsh (Basinger, 1976a). Unlike the Princeton chert, however, much of the original carbon is gone from the Indian specimens. Study must therefore be carried out using thin-sectioning techniques (Sahni, 1943; Chitaley, 1955; Paradkar, 1973) which are not only time-consuming but limit the type and amount of information that can be obtained. Due to the generally thicker nature of thin-sections, fine cellular details are often obscured and difficult to see, especially in photographed material.

The Princeton chert locality is exposed on the east bank of the Similkameen River about 8.4 km SSW of the town of Princeton, British Columbia. Boneham (1968) initially referred to the site as "locality I," whereas Basinger (1976a) renamed it the "Ashnola locality". The site is now known as the "Princeton chert" or "Princeton chert locality" (e.g., Basinger & Rothwell, 1977; Basinger, 1981; Basinger, 1984; Stockey, 1984). The outcrop consists of a 10 m thick section of interbedded chert and coal layers (Basinger, 1976a). Boneham (1968) determined the stratigraphic position at about 550 m above the Princeton-Black coal seam and recognized 35 chert and 33 coal layers. Basinger (1976a) found that many of the chert or coal layers anastomose making it difficult to identify specific layer numbers. Using the layers of greatest thickness and lateral extent as markers, Basinger (1976a) subsequently divided the locality into 9 intervals. However, more recently Stockey (1987), has been able to identify and systematically sample 49 chert layers.

The Princeton locality is in the Princeton Basin and is part of the Allenby Formation (Boneham, 1968). The Princeton Basin is only one of many small Tertiary basins within the Interior Plateau of south-central British Columbia (Shaw, 1952; Boneham, 1968; Wilson, 1977b). It covers an area of about 170 sq. km and structurally represents a complex half graben filled with strata of the Princeton Group (McMechan, 1983). Although Dawson (1879) provided the first detailed published account of the geology of the Princeton area, Bauerman (1884) was the first to record the presence of Tertiary deposits in this region. A more recent review of the geology of the Princeton Basin is provided by McMechan (1983).

Exposures of Tertiary strata are found throughout southern British Columbia not only in structural basins, but in fault troughs, pre-existing topographic depressions, and residual caps on hilltops surrounding the basins (McMechan, 1983). However, lack of good outcrop exposures (less than 1% of overall basin area) has hampered and confused detailed stratigraphic correlations of the Tertiary rocks

(McMechan 1983). Dawson (1879), Camsell (1907), and Rice (1947) interpreted the Tertiary stratigraphy of the Princeton map-area (Rice, 1947) to consist of upper and lower volcanic beds separated by sedimentary rocks. Rice (1947) formally designated these lavas and sediments as the Princeton Group. Shaw (1952) subdivided the the Princeton Group into the Upper Volcanic, Allenby, and Lower Volcanic Formations. Strata of the Princeton Group lie unconformably on the Upper Triassic Nicola Group, Lower Cretaceous Kingsvale Group, and intrusive rocks of different ages (McMechan, 1983).

Rice (1947) and Shaw (1952) placed the Upper Volcanic Formation above the Allenby Formation, but Hills (1962, 1965a) later found that the Upper Volcanic Formation was a laterally discontinuous unit lying below the lower strata of the Allenby Formation and therefore considered it to be part of the Allenby Formation (Hills, 1965b). This volcanic unit has since been referred to informally as the "volcanic member" of the Allenby Formation (McMechan, 1983) and the Princeton Group consists of the Lower Volcanic and Allenby Formations (Preto, 1972; McMechan, 1983).

The Allenby Formation was formally named and described by Shaw (1952) for strata composed mainly of "massive, cross-bedded granule and pebble conglomerate, sandstone and massive and thinly bedded shale, with intercalated beds of coal, carbonaceous siltstone and shale, and bentonite" exposed along the banks of the Similkameen River near the now abandoned town of Allenby. Hills (1962, 1965b) included lavas and breccias of Shaw's Upper Volcanic Formation as part of the Allenby Formation, stating that these occur interbedded with the sedimentary strata in the lower part of the Allenby Formation. Two sedimentary "members" and a "volcanic member" are currently recognized based on gross stratigraphic relationships in the southern portion of the Princeton Basin; however, lack of distinctive markers in the basin north of Hills' (1962) Rainbow Lake anticline makes subdivision difficult in this region (McMechan, 1983). The two sedimentary "members" are further broken down into an upper "coal-bearing member" and "lower member" characterized by a mixture of volcaniclastic and arkosic sedimentary rocks with few occurrences of coal (McMechan, 1983). The Princeton chert locality is within the "coal-bearing member" about 550 m above the Princeton Black-Blue Flame coal zone (Boneham, 1968).

Deposition of the Allenby Formation has occurred primarily in fluvial environments (McMechan, 1983). Coarser sediments in the northern part of the basin suggest that these were deposited in a high energy braided river system, whereas finer sediments in the south represent a lower energy meandering river environment with related subenvironments such as backswamps, overbank/floodplains, and lakes (McMechan, 1983).

Until recently, the age of the Allenby Formation has been in dispute. Plants collected from Princeton sediments were correlated with the flora of the Upper Eocene to Lower Oligocene Kitsilano Formation of Vancouver by Berry (in Rice, 1947), but Rice (1947) considered the age to be Upper Oligocene or Lower Miocene in accordance with Bell, who compared the Allenby flora to the Upper Oligocene-Lower Miocene Bridge Creek flora of the Jonn Day Basin in Oregon (in Rice, 1947). The Bridge Creek flora is now considered to be early Oligocene in age (Wolfe, 1981). An Upper Oligocene-Lower Miocene age was further supported based on a collection of fossil insects identified by Carpenter (in Rice, 1947).

However, a mammal tooth, belonging to the genus Trogosus Marsh, order Tillodontia, suggests a Middle Eocene age for the Allenby Formation (Russell, 1935; Gazin, 1953). A Middle Eocene age has also been suggested based on the presence of the dispersed pollen taxon Pistillipollenites macgregorii Rouse (Rouse & Srivastava, 1970); however, the extended geologic range of this pollen type into Paleocene (Crepet & Daghlian, 1981) and Cretaceous sediments (Crepet, 1984) restricts its use as an index fossil for Lower and Middle Eocene strata. A Middle Eocene age has been more firmly established for the Allenby Formation based on K-Ar dates from volcanic rocks within the Allenby Formation (Rouse & Mathews, 1961; Mathews & Rouse, 1963; Mathews, 1964; Hills & Baadsgaard, 1967), palynological correlations (Rouse et al., 1971; Mathews & Rouse, 1984), and studies of fossil insects and freshwater fishes (Wilson, 1977a, b, 1978, 1980, 1982, 1988).

Chert samples from the Princeton locality were first collected by Arnold and Boneham (Basinger, 1976a), but were used for pollen and spore analysis (Boneham, 1968). Specimens of chert were later given to Miller (1973) who described an ovulate pine cone, Pinus arnoldii, and associated leaves and twigs, P. similkameenensis. Several years later a general survey documenting the diversity of chert plants was made by Basinger (1976a). Subsequent studies focused primarily on the coniferous remains. Rothwell (1975) and Rothwell & Basinger (1979) described a new species of pollen cone, Metasequoia milleri, while description of the vegetative organs and ovulate cones of M. milleri followed (Basinger, 1981, 1984). Stockey (1984) added to the conifer flora with descriptions of the ovulate cone, Pinus princetonensis, and leaves, P. andersonii.

Study of the Princeton chert angiosperm remains is in its infancy. A concentrated effort to describe the angiosperms began in the mid-1980's with a study of the fruits and seeds (Cevallos-Ferriz, 1987). This study showed the utility and importance of fruit and seed anatomy in determining the affinities of these fossils. Families represented by these remains now include Lythraceae (Cevallos-Ferriz & Stockey, 1988a), Araceae (Cevallos-Ferriz & Stockey, 1988b), Nymphaeaceae (Cevallos-Ferriz & Stockey, 1989), Vitaceae (Cevallos-Ferriz & Stockey, 1990a), and Rosaceae (Cevallos-Ferriz & Stockey, 1990d). However, prior to 1987 the only angiosperms formally described from the chert were a semiaquatic dicotyledonous rhizome of unknown affinity, Eorhiza arnoldii Robison & Person (1973), and a rosaceous flower, Paleorosa similkameenensis Basinger (1976b).

Subsequent investigations of the Princeton angiosperms have yielded a far more diverse and exquisitely preserved flora than initially recognized (Basinger, 1976a; Basinger & Rothwell, 1977). Numerous flowers occur in the chert (Stockey, 1987). In addition to Paleorosa, two types of flowers with in situ pollen have been described. Wehrwolfea striata Erwin et Stockey shows affinities with the Sapindaceae (Erwin & Stockey, 1990a), while the familial relationships of the other flower, Princetonia allenbyensis Stockey (1987), remains uncertain. In addition to the floral remains, wood fragments of Magnoliaceae (Cevallos-Ferriz & Stockey, 1990c) and Rosaceae (Cevallos-Ferriz & Stockey, 1990b) have also been described. However, large numbers of unidentified twigs, leaves, and roots have not yet been thoroughly investigated.

The present study was undertaken to describe and assess the affinities of monocotyledons in the Princeton chert. Nine different types of vegetative remains representing stems with attached leaves and roots, plus isolated stems, laminae and roots have been recognized. Four of the most complete and abundant monocotyledons in the chert are described and discussed here. Among these are a petiole showing affinities with the Alismataceae (Erwin & Stockey, 1989a), rhizomes with internal structure comparable to the order Liliales (Erwin, 1989b; Erwin & Stockey, 1990b), the vegetative body of a small monocotyledonous plant with leaf anatomy similar to the extant families Cyperaceae and Juncaceae (Erwin & Stockey, 1990d), and a rhizomatous coryphoid palm showing similarities in vegetative anatomy to the three extant coryphoid genera Rhapidophyllum Wendland & Drude, Brahea Martius, and Serenoa J.D. Hooker (Erwin, 1987; Erwin & Stockey, 1990c).

As in most extant floras, the majority of angiosperms in fossil floras are dicotyledons (Daghlian, 1981). The Princeton chert is no exception in this respect; however, results from the present investigation show that the Princeton chert locality is a unique site not only in yielding a relatively abundant monocot flora, but the plant remains are anatomically-preserved, a rare occurrence in the fossil record. The low energy depositional environment represented by the Princeton chert site has preserved two of the monocotyledons as nearly intact plants rooted in situ. Since these plants have a short, rosette or rhizomatous growth form they are more easily preserved as whole plants. This provides the opportunity to base taxonomic and systematic considerations on nearly whole plants rather than disarticulated organs. Such an approach decreases the likelihood that isolated vegetative organs of these plants will be described and named as different taxa, therefore, giving a more accurate picture of the actual diversity of monocotyledons in the Princeton chert.

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Chapter 2: Permineralized monocotyledons from the Middle Eocene Princeton chert (Allenby Formation) of British Columbia: Alismataceae.*

Introduction

Plant remains indicative of an aquatic environment are among some of the most abundant megafossils described from the Middle Eocene Princeton chert locality. These remains include: the semiaquatic aerenchymatous rhizomes of the monocot-like dicotyledon, Eorhiza arnoldii Robison and Person (1973, Stockey and Cevallos-Ferriz 1987), stems and petioles of the fern Dennstaedtiopsis aerenchymata Arnold and Daugherty (Basinger 1976), fruits and seeds described as Decodon allenbyensis (Cevallos-Ferriz and Stockey 1988a) that compare anatomically to fruits and seeds of the extant, D. verticillatus (L.) Ell., and nymphaeaceous seeds, Allenbya collinsonae Cevallos-Ferriz and Stockey (1988b).

In the present study, a small monocot axis is described having anatomy similar to that found in petioles of the Alismatales, resembling most closely those of the Alismataceae and Butomaceae. The Alismatales as defined here include three families: the Alismataceae, Butomaceae, and Limnocharitaceae (Takhtajan 1966; Cronquist 1981; Tomlinson 1982). Although the Alismatales today represent one of the most familiar and widespread groups of aquatic and semiaquatic plants (Sculthorpe 1967), their fossil history is poorly known. Daghlian (1981) reviewed the fossil record of the order noting that the group has a reliable record dating back to the Oligocene; however, reports of fossil leaves and fruits from older sediments (Berry 1925; Brown 1962;

*A version of this chapter is published in Can. J. Bot. 67:2636-2645.

Doyle 1973; Hickey and Doyle 1977) are dubious, as is the fossil pollen record. Muller (1981) reviewed the pollen record citing several alismatacean pollen types from Cretaceous and Tertiary deposits, but regards these reports as "pending" until further documented.

The discovery of a well preserved monocot axis in the Middle Eocene Princeton chert showing anatomical features of the Alismatales has allowed recognition of a new genus and species assignable to the Alismataceae, Heleophyton helobioides Erwin & Stockey gen. et sp. nov. Furthermore, presence of the family in western North America during the early Tertiary not only adds to our knowledge of fossil monocotyledons, but provides additional evidence to support the interpretation that the Princeton locality represents an aquatic system, a site ideal for the study of monocot evolution.

Materials and methods

One small permineralized axis showing numerous vascular bundles scattered in lacunose ground tissue has been found in a chert block from the Princeton chert locality. The locality is part of the Allenby Formation that outcrops on the east bank of the Similkameen River, 8 km south of the town of Princeton, British Columbia. Chert deposits are part of the Princeton Group 650 m above the Princeton Black coal seam (Boneham 1968) and consist of 49 interbedded chert and coal layers with an occasional thin bed of ash (Cevallos-Ferriz and Stockey 1987). The locality has been referred to as locality "I" (Boneham 1968) and the "Princeton chert" (Basinger and Rothwell 1977; Stockey 1984). Based on K-Ar dating (Hills and Baadsgaard 1967) and studies of freshwater fish (Wilson 1977, 1982), the Princeton chert has been dated Middle Eocene.

The specimen was studied using a modified cellulose acetate peel technique and hydrofluoric acid (Basinger & Rothwell 1977; Basinger 1981). Peel sections were mounted on microscope slides with Coverbond xylene soluble mounting medium for microscopic examination. Nineteen sections were made, twelve consecutive transverse and seven longitudinal sections.

Bundle morphology of the fossil petiole was compared to that of extant Echinodorus cordifolius (L.) Griseb. (ALTA. 19681, Bird 368). Dried petioles were boiled in water for several minutes (Tomlinson 1961), fixed in formalin acetic acid and alcohol (FAA), dehydrated in 10, 30, 50, 70, 90, 100% EtOH, followed by a tert-butyl alcohol (TBA) series. Paraplast Plus medium was used for infiltration and embedding. Sections 10 um thick were cut on a rotary microtome and stained with safranin-fast green (Johansen 1940). Slides of fossil and extant specimens are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Results

Systematic Description

Subclass: Alismatidae

Order: Alismatales

Family: Alismataceae

Genus: Heleophyton Erwin et Stockey gen. nov.

Species: Heleophyton helobioides Erwin et Stockey sp. nov.

Diagnosis: Petiole small, 1.8 mm X 1.5 mm wide, rectangular with rounded corners, two lateral sides with central rib flanked by a groove. Epidermis single layered, lacking stomata, glands, trichomes, and hydropoten; cells square to rectangular, radially elongated in transverse section, 12.0-18.0 um radially X 6.0-18.2 um tangentially, some cells elongated axially, up to 36 um long; cell walls thin, radial walls either straight or undulate. Hypodermis one to two cells thick; cells thick-walled with simple pits, additional thicker walled sclereids and small rudimentary bundles scattered in hypodermis. Ground tissue lacunose; lacunae numerous, evenly distributed throughout ground tissue, separated by uniseriate partitions of thin-walled parenchyma three to five cells long; occasionally cells of partitions replaced by thick-walled cells with simple pits and groups of four to 7 cells ca. 6-9 um in diam. with helical thickenings on lateral walls; diaphragm-like structures of small diameter parenchyma traverse some lacunae. Ground tissue including scattered tannin cells; transverse veins common, containing cells with helical thickenings. Vascular bundles collateral, numerous, circular to oval in transverse section, in five distinct series: 1) 11-13 bundles in central V-shaped arc, 2) an abaxial arc of 6 bundles, 3) two peripheral abaxial arcs with three bundles each, 4) a peripheral abaxial series of two bundles, and 5) an adaxial semi-circular series of 7 bundles with inverse orientation of vascular tissue to bundles in series one through four. Protoxylem lacuna 15.0-21.0 um wide, protoxylem elements, with annular to helical secondary wall thickenings. Metaxylem elements thin-walled, 27.0-33.0 um wide, helical to scalariform, some cells without distinct thickenings, including tyloses. Phloem a single semicircular strand; cells thin-walled, end walls transverse to slightly oblique, sieve areas or sieve plates not observed; some cells with tannin-like contents. Holotype: P2313 Btop

Etymology: From the Greek _Heleo_ (_Heleos_ gen.) = marsh, and _phyton_ = plant. The specific epithet refers to the subclass Helobiae _sensu_

Tomlinson (1982) (Alismatidae of Cronquist), and the Greek oides = denoting likeness of form.

Description

General features

The axis, 1.8 mm X 1.5 mm wide X 1.5 mm long (Pl. II, 1 Fig. 1), exhibits anatomical features similar to those found in petioles of the Nymphaeales and Alismatales. In transverse section, the shape of the axis is roughly a rectangle with rounded corners and shows approximately 36 circular to oval-shaped vascular bundles scattered throughout an aerenchymatous ground tissue. Located on each lateral side is a rib-like area flanked on either side by a groove or channel (Pl. II, 1 Fig. 1, arrows).

Vascular tissue

The following distinct series of bundles are recognized: 1) a median V or U-shaped arc of 11-13 vascular bundles with one large central bundle (Pl. II, 1 Fig. 1, Pl. II, 3 Fig. 24) and five to 6 lateral bundles that decrease in size becoming more closely-spaced as they extend toward the adaxial surface (Pl. II, 1 Fig. 1, Pl. II, 3 Fig. 24); 2) an abaxial series of 6 more widely-spaced vascular bundles that lie below the main arc (Pl. II, 1 Fig. 1, Pl. II, 3 Fig. 24); 3) two short abaxial arcs with three bundles each, 4) two bundles which lie just below the abaxial epidermis (Pl. II, 1 Fig. 1, Pl. II, 3 Fig. 24), and 5) a semicircular adaxial series composed of 7 bundles with protoxylem oriented toward the abaxial surface rather than the adaxial surface as in bundles of series one to four (Pl. II, 1 Fig. 1, Pl. II, 1 Fig. 4, Pl. II, 3 Fig. 24). In addition, small circular rudimentary bundles composed of thin-walled cells surrounded by thick-walled fibers are found in the hypodermis (Pl. II, 1 Figs. 1-3, Pl. II, 3 Fig. 24).

In transverse section, vascular bundles are single, collateral, circular to oval-shaped, up to 0.17 mm radially X 0.10 mm tangentially and surrounded by a parenchymatous sheath (Pl. II, 1, Figs. 4-7). In larger bundles, vascular tissue consists of a single relatively large semicircular phloem strand and a lacuna 15.0-21.0 um in diameter that marks the former position of the protoxylem (Pl. II, 1 Figs. 4, 6, 7). Each lacuna is surrounded by a ring of 9-14 thin-walled cells that are three to five-sided in transverse section. Three and four-sided cells are triangular in transverse section with the tip of the triangle closest to the lacuna, the base curved out away from the lacuna (Pl. II, 1 Fig. 7). Some lacunae appear to be filled with dark contents (Pl.II, 1 Figs. 4, 7); however, the dark appearance is due to the thickened inner tangential cell walls that lie adjacent to the lacuna (Pl. II, 1 Fig. 8). Adhering to the inner walls of some lacunae are the remains of protoxylem elements (Pl. II, 1 Fig. 8). These elements are about 7.2 um wide and show annular to helical secondary wall thickenings (Pl. II, 1 Fig. 8).

Situated between the protoxylem lacuna and phloem of larger vascular bundles are two to three circular thin-walled metaxylem elements, 27.0-33.0 mm wide (Pl. II, 1 Fig. 7). As seen in longitudinal section, these cells have relatively thin walls and show no distinct secondary wall thickenings (Pl. II, 1 Fig. 8); however, as pointed out by several authors (i.e. Arber 1920; Stant 1964; Sculthorpe 1967; Tomlinson 1982), reduction in lignification of tracheary elements is a common feature of aquatic plants and may account for the thin-walled appearance of these cells. Figure 9 shows cells with helical wall thickenings about 20 um wide that may represent metaxylem elements; however, in the Alismatales, scalariform and reticulate pitting is predominant in metaxylem while annular and helical thickenings characterize protoxylem (Stant 1964). Spherical structures that probably represent tyloses are found inside the thin-walled metaxylem elements (Pl. II, 1 Figs. 7, 8). Tyloses are commonly found in non-functioning secondary xylem, but have also been reported in the primary xylem of young oat coleoptiles (Esau 1977).

Phloem is composed of thin-walled cells ranging in diameter from 4.6 - 11.0 um (Pl. II, 1 Figs. 7, 10). Although none of these cells show distinct sieve areas, sieve plates, or companion cells, several cells in longitudinal section do have transverse to slightly oblique end walls that may represent sieve plates (Pl. II, 1 Fig. 10). However, because parenchyma is a common component of phloem, some of these cells may be parenchyma rather than sieve tube elements. Located at the periphery of and in the phloem are thin-walled cells that contain dark brown contents (Pl. II, 1 Figs. 5, 7, 10) that probably represent tannin cells. Thick-walled fibers at the periphery of the phloem and flanking cells that surround the protoxylem lacuna, are most prominent in smaller peripheral bundles where they nearly ensheath the vascular tissue (Pl. II, 1 Figs. 5, 7).

Ground tissue

Ground tissue is aerenchymatous (Pl. II, 1 Fig. 4, Pl. II, 2 Fig. 11) with numerous evenly distributed lacunae that are circular to oval in transverse outline, and delimited by uniseriate partitions (occasionally two cells wide) of thin-walled ground tissue, three to five cells long. Lacunae are of nearly equal diameter tending to be slightly wider toward the center of the axis. Some lacunae are completely traversed by or have remnants of diaphragm-like structures composed of thin-walled cells smaller in diameter than the surrounding ground tissue parenchyma (Pl. II, 2 Fig. 12). Throughout the ground tissue some cells of the partitions contain a dark brown material (Pl. II, 2 Figs. 11, 13) and probably represent tannin cells. Other cells are thick-walled with simple pits and probably represent sclerified parenchyma (Pl. II, 2 Fig. 14). At two different partition junctions are small groups of four to 7 narrow cells 6-9 um in diameter that show thickened walls with faint bar-like thickenings that represent either transverse veins in cross section or rudimentary bundles of the axial system (Pl. II, 2 Fig. 15).

Transverse veins connecting adjacent vascular bundles commonly traverse ground tissue, appearing in longitudinal section as direct extensions from vascular bundles or separate incomplete strands (Pl. II, 1 Fig. 6, Pl. II, 2 Fig. 16). Veins consist of a group of several narrow cells with helical thickenings, some branch (Pl. II, 1 Fig. 6, Pl. II, 2 Fig. 16), and they appear to run parallel to or within ground tissue partitions.

Epidermis and subepidermal layers

The epidermis is a single layer composed of cells that in regions of minimal distortion are square to rectangular in transverse and longitudinal section. In transverse section, rectangular cells are radially elongated. Cells are 12.0-18.2 um radially X 6.0-18.0 um tangentially X 6.0-36.0 um axially and have thin radial and inner tangential walls while the outer tangential wall appears thicker, possibly due to the presence of a cuticle (Pl. II, 2 Figs. 17-20). In some cells the radial walls are sinuous rather than straight (Pl. II, 2 Figs. 17, 20). No stomata, trichomes, hydropoten, or glands have been found in the epidermis; however, several sections of the epidermis are composed of thick-walled cells (Pl. II, 2 Fig. 19). Thick-walled cells with simple pits form a one to two layered hypodermis that is discontinuous laterally and axially by interruption of thin-walled ground tissue (Pl. II, 1 Fig. 2, Pl. II, 2 Figs. 17, 18). Interspersed among hypodermal cells are small groups of very thick-walled cells with simple pits that resemble brachysclereids (Pl. II, 1 Fig. 3, Pl. II, 2 Fig. 21).

Discussion

Anatomy of the fossil petiole most closely resembles the monocot order Alismatales, but also shares structural features with the dicot order Nymphaeales (sensu Cronquist 1981). In light of the controversy over the phylogenetic relationship between the Nymphaeales and Alismatales (Tomlinson 1982) comparison of the fossil to nymphaealean genera is presented.

Ground tissue in Heleophyton helobioides consists of numerous evenly distributed lacunae separated by uniseriate partitions of thin-walled parenchyma, similar to that found in Nuphar (Nymphaeaceae) (Solereder 1908; Kostyniuk 1970), whereas aerenchyma in Cabomba and Brasenia (Cabombaceae) has 8-12 large lacunae that surround centrally located vascular bundle-pairs (Kostyniuk 1970; Moseley et al. 1984). Two to four large lacunae with smaller peripheral lacunae characterize Nymphaea, Euryale, and Victoria (Nymphaeaceae) (Conard 1905; Kostyniuk 1970), while there are four large lacunae in Nelumbo (Nelumbonaceae). Unlike the lacunae in Heleophyton, lacunae of the Cabombaceae, Nymphaeaceae, and Nelumbonaceae are separated by multiseriate partitions of ground tissue (Solereder 1908). In Barclaya (Barclayaceae), no major air cavities have been reported (Kostyniuk 1970).

The large central bundles in Heleophyton have a protoxylem lacuna surrounded by a distinct ring of thin-walled ground tissue cells, thin-walled xylem with annular, helical and scalariform wall thickenings, and a well developed phloem strand (Pl. II, 3 Fig. 26). Simple bundles like these are found in Nuphar and Barclaya; whereas in the Cabombaceae, Nymphaea (Pl. II, 3 Fig. 27), Euryale, and Victoria, the vascular system includes a mixture of simple and double bundles. Double bundles contain two phloem strands separated by a common protoxylem lacuna (Conard 1905; Kostyniuk 1970; Metcalfe and Chalk 1950; Moseley et al. 1984). Bundles of Nelumbo are morphologically unique for the order and occur scattered throughout the partitions of ground tissue. They are characterized by one to three large tracheary elements, no protoxylem lacunae, and several laticifers between the tracheary elements and phloem (Esau and Kosakai 1975; Ito 1986).

Bundles in Heleophyton are arranged in five distinct series. The protoxylem of series (1-4) are directed toward the adaxial surface, (i.e. normally oriented) whereas protoxylem of series (5) is directed toward the abaxial surface (i.e. inverted) (Pl. II, 1 Fig. 4, Pl. II, 3 Fig. 24). Although bundle morphology is similar to Nuphar, bundle distribution in Nuphar consists of a single peripheral series of bundles with protoxylem directed toward the center of the petiole and three to many centrally-located bundles with randomly oriented protoxylem (Kostyniuk 1970). In Barclaya, bundles are arranged in a central ring with protoxylem directed toward the center. Therefore, although the ground tissue and bundle morphology in Heleophyton show some similarities to the Nymphaeales, distribution of ground tissue lacunae and vascular bundles is different.

Plants combining features of Heleophyton occur in the aquatic to semiaquatic monocot order Alismatales. The three families comprising the Alismatales: Alismataceae, Butomaceae (sensu Pichon 1946), and Limnocharitaceae show a close relationship to one another as evidenced by similarities in vegetative morphology, anatomy, floral morphology and development (Tahktajan 1980; Tomlinson 1982). The Limnocharitaceae differs from Heleophyton in bundle morphology, distribution, possession of laticifers, and scarcity of tannin development.

In Heleophyton as mentioned above, the vascular bundles are arranged in five series. In the Butomaceae, the vascular system also consists of five series: 1) a median V-shaped arc of 9 major bundles, comparable to the median arc of Heleophyton, 2) an abaxial arc of three bundles, 3) a single bundle in the abaxial angle of the leaf, 4) a peripheral hypodermal series of numerous bundles, those of the adaxial surface inverted, and 5) minute or rudimentary bundles or fibrous strands distributed throughout the central ground tissue (Stant 1967; Tomlinson 1982). In contrast to Heleophyton, Butomus lacks a separate distinct series of inverted bundles in the adaxial ground tissue (i.e. series V of Heleophyton) and has numerous rudimentary bundles or fibrous strands composed of 6-12 small fiber-tracheids with spiral thickenings at partition junctions throughout the ground tissue, essentially taking the place of laticifers in the Alismataceae (Stant 1967). Similar groups of four to 7 small diameter thick-walled cells with helical thickenings are present in Heleophyton, but were found at only two partition juhctions (Pl. II, 2 Fig. 15). Stant (1967) refers to these groups of cells as rudimentary bundles or fibrous strands in Butomus, but does not mention the possibility that they may represent sections through transverse veins, perhaps because in the Alismatales transverse veins are included in the diaphragms, and therefore would not appear in partition junctions, but rather in lacunae. In Heleophyton the transverse veins appear to run parallel to or within partitions, and therefore it is possible that these groups of cells are transverse veins in cross section rather than rudimentary bundles of the axial system.

Arrangement of vascular bundles in the Alismataceae, particularly certain species of Sagittaria L. (Pl. II, 3 Fig. 22) and Echinodorus Micheli (Pl. II, 3 Fig. 23), is most similar to Heleophyton. In the four Sagittaria species studied by Stant (1964), all have bundles arranged in three series: 1) a median arc of three to five bundles in smaller leaved species such as S. sagittaria L. and S. japonica, while in larger leaved species more numerous bundles may be found, 2) one to many abaxial arcs containing many bundles, the number dependent on petiole size and the level from which a section is taken, and 3) an adaxial series of three inverted bundles with additional peripheral bundles. Distribution of bundles in S. montevidensis (Pl. II, 3 Fig. 22) resembles that of Heleophyton if vascular bundle N is included in series III; however, the adaxial series (V) of the two differs in number and arrangement of bundles.

Bundle distribution in Heleophyton is most comparable to that of Echinodorus macrophyllus (Kunth) Micheli illustrated by Meyer (1932, 1935). Using the labelling scheme of Meyer, bundles in *E. macrophyllus* (Pl. II, 3 Fig. 23) are in five series: I) a median arc of 7-9 normally oriented bundles, II) an abaxial arc of up to 10 normally oriented bundles, III) two small abaxial arcs with three bundles each, IV) a peripheral abaxial series of two small bundles, and V) an adaxial series of three to five inverted bundles. In addition, there is an isolated bundle N just below series II. *Heleophyton* differs from *E. macrophyllus* by having 11-13 bundles in the main arc (I) rather than 7-9. With respect to series II, *E macrophyllus* has 10 bundles as opposed to 6 in *Heleophyton*. Below series II, there is an isolated bundle (N) in *E. macrophyllus* that corresponds to a bundle in the same position in *Heleophyton*. Series III of *E. macrophyllus* and *Heleophyton* consists of two peripheral arcs of three bundles each. Two of the three bundles in each series of *Heleophyton* are nearly the same size and larger than the third which lies at the periphery of the petiole; whereas in *E. macrophyllus*, there is one large bundle and two smaller bundles. Two abaxial bundles comprise series IV in both species with bundles in *Heleophyton* nearly the same size as the bundles in series I to III. Bundles of series IV in *E. macrophyllus*, on the other hand, are quite small relative to other bundles (Pl. II, 3 Fig. 23). The adaxial series in both extant species is here designated as V (Pl. II, 3 Figs. 22-24). In *Heleophyton*, this series consists of 7 inverted bundles in a semicircular pattern, while in *E. macrophyllus* it consists of five inverted bundles in a pentagonal arrangement. However, a similar semicircular pattern can be seen in *E. macrophyllus* if two of the peripheral bundles are included in this series (Pl. II, 3 Fig. 23, solid lines).

Despite similar vascular bundle distribution in Heleophyton and E. macrophyllus, morphology of the larger central bundles of the major arc differs between the two. In transverse section, the central bundles of E. macrophyllus are nearly circular and have a large protoxylem lacuna almost completely surrounded by a single wide U-shaped arc of metaxylem elements that is flanked abaxially by a shallow U-shaped phloem strand composed of two rows of alternating sieve tubes and companion cells (Pl. II, 3 Fig. 25). Vascular bundles of this type are found consistently throughout the Alismataceae (Stant 1964). The larger central bundles of Heleophyton however, most closely resemble bundles of Butomus in size and structure (Pl. II, 3 Fig. 28). They are ovate in transverse section with a narrow diameter protoxylem lacuna, have one to three metaxylem elements arranged in a more less straight line between the protoxylem lacuna and adaxial surface of the phloem. Phloem consists of a semicircular strand containing indistinct sieve tubes and companion cells.

Based on a combination of available anatomical characters, the fossil petiole described here, Heleophyton helobioides Erwin and Stockey gen. et sp. nov., shows features commonly found in families of the aquatic to semiaquatic Alismatidae. Similarities include aerenchymatous ground tissue consisting of numerous evenly distributed lacunae delimited by uniseriate partitions of thin-walled parenchyma that includes remnants of diaphragm-like structures, tannin cells, and vascular bundles arranged in distinct U or V-shaped arcs with bundles of the adaxial series inversely oriented. Heleophyton has been assigned to the Alismataceae based primarily on similarity of bundle distribution to that of Sagittaria and Echinodorus; however, because bundle structure is more like Butomus, a new genus Heleophyton is proposed for the fossil petiole.

The fossil record of the Alismatales is poorly represented being known primarily from leaf compressions and molds and casts of fruits and seeds. Tahktajan et. al. (1963) reported seeds referable to the Butomaceae from Oligocene to Pliocene deposits of Russia. Sagittate leaf compressions with campylodromous venation assigned to Alismaphyllum victor-masonii (Ward) Berry (1911) are found in the Lower Cretaceous Potomac Group; however, this leaf type characterizes other monocotyledon families (Doyle 1973; Hickey and Doyle 1977). A Lower Cretaceous leaf fragment described by Saporta (1894) as Alismacites primaevus from Portugal is also of questionable affinity as is Alismaphyllum cretaceum from the Upper Cretaceous Ripley Formation (Daghlian 1981). Brown (1962) assigned leaves Alismaphyllites grandifolius and associated fruits, Sagittaria megaspermum, from the Paleocene to the Alismataceae. Definitive alismatacean megafossils, however, until now have not been documented earlier than the Oligocene (Daghlian 1981). Alisma-like fruits are reported from the Oligocene of England (Chandler 1964) and Miocene of Russia, while Alisma-like fruits and seeds, and fruits of Caldesia Parl. and Sagisma Nikitin are known from the Oligocene of Russia (Dorofeev 1963; Tahktajan et al. 1963; Daghlian 1981). Achenes similar to Caldesia have also been reported from the Tertiary of Europe by Tiffney (1985) but so far have not been described.

Like much of the megafossil record, the fossil pollen record is also dubious. All of the alismatacean pollen types cited by Muller (1981) are pending further documention. Tahktajan et al. (1963)

reported *Butomus*-like pollen from Neogene sediments of the Aral region and the Miocene of Caucasus. Pollen similar to *Alisma* has been described from the Oligocene of Belgium (Roche and Schuler 1976), central Europe (Krutzsch 1966), and the Upper Miocene of France (Naud and Suc 1975). Cretaceous species, *Cretacaeiporites scabratus* (Herngreen 1973) from Brazil is similar to *Alisma*, while *Punctioratipollis krutzschi* (Boltenhagen 1975) from Gabon is similar to *Sagittaria*.

Daghlian (1981) has suggested that the Alismataceae was a Tertiary development dating from the Oligocene or possibly the Paleocene. The discovery of a petiole with a vascular system showing an alismatacean bundle distribution in the Middle Eocene of North America supports this idea; however, the petiole has Type I bundles similar to those in *Butomus* which suggests that the petiolar vasculature of the Alismataceae as is known today may not have fully evolved until some time later, perhaps in the Oligocene. According to Cheadle and Uhl's (1948) classification of monocot bundles, Type I bundles are regarded as the most primitive among monocotyledons. Finding Type I bundles in *Heleophyton* tends to support this conclusion or at least documents this bundle type in the Middle Eocene. Furthermore, it provides evidence that protoxylem lacunae had evolved in aquatic or semiaquatic plants by Middle Eocene time.

Based on the presence of turtle bones and plant remains with features indicative of a wet environment, the Princeton chert locality has been interpreted as a quiet lake or marsh surrounded by temperate to subtropical vegetation (Cevallos-Ferriz 1987). The discovery of *Heleophyton* in the chert flora provides further evidence for this interpretation. As is typical in most aquatic to semiaquatic plants, *Heleophyton* has aerenchymatous ground tissue and vascular bundles with protoxylem lacunae, reduced thin-walled tracheary elements, and a relatively large phloem strand. Well preserved aerenchyma is also found in leaves and rhizomes of other chert plants such as the monocot-like dicotyledon, *Eorhiza arnoldii* (Robison and Person 1973; Stockey and Cevallos-Ferriz 1987) and the fern *Dennstaedtiopsis aerenchymata* Basinger 1976). The taxonomic affinity of *Eorhiza* is still not known but its abundance and rhizomatous habit suggest that it could have formed extensive stands in marshy habitats along lake margins. Lythraceous seeds described as *Decodon allenbyensis* Cevallos-Ferriz and Stockey are very similar to seeds of the extant swamp willow *D. verticillatus* (Cevallos-Ferriz and Stockey 1988a). *Decodon verticillatus* today is found in subtropical regions along shorelines of marshes, lakes, and rivers and therefore it is possible that a similar habitat supported *D. allenbyensis*. Numerous nymphaeaceous seeds and one fruit with seeds described as *Allenbya collinsonae* Cevallos-Ferriz and Stockey (1988b), is closely related to the Nymphaeaceae and is evidence of an aquatic family (Cevallos-Ferriz and Stockey 1988b).

The presence of a petiole with a vascular system similar to that of the Alismataceae showing bundles with a protoxylem lacuna and reduced thin-walled xylem, suggests that *Heleophyton* may have grown either as an emergent or submerged aquatic with floating leaves, perhaps in association with the nymphaeaceous plant. The latter habit is suggested by the thickening of the inner tangential walls of the cells that lie adjacent to the protoxylem lacunae. Thickening of these walls is a common phenomenom in submerged Alismatidae (Tomlinson 1982) and as a result the lacunae probably function in water conduction (Denny 1980; Tomlinson 1982; Ito 1983). Although not conclusive, Heleophyton lacks stomata in the epidermis which could also be indicative of a submerged habit.

As study of the Middle Eocene Princeton chert flora continues, its significance as a locality yielding early monocotyledonous remains is becoming more evident. Among the monocot-like remains now known are a petiole with a vascular system similar to that of the aquatic to semiaquatic order Alismatales and nymphaeaceous genera, thousands of seeds related to the nymphaeaceous genus Victoria, and a monocot-like dicot, Eorhiza arnoldii, that has rhizomes with secondary xylem, but monocotyledonous leaves. Further investigations of the chert should yield more complete specimens of these plants, enabling whole plant reconstruction, and most importantly providing fossil evidence for answering questions of monocot phylogeny that are currently based primarily on comparative morphology and anatomy of extant plants.

Plate II, 1

Heleophyton helobioides gen. et sp. nov., petiole.

Fig. 1. Transverse section showing general outline, vascular bundle distribution, and aerenchymatous ground tissue. Note lateral ribs and possible channels (arrows). Arrowhead indicates central vascular bundle of median arc. P2313 Btop # 0. X 54.

Fig. 2. Transverse section showing small hypodermal vascular bundles (arrows), and lateral discontinuity in hypodermis between thin-walled ground tissue and sclerified parenchyma cells. P2313 Btop # 0. X 200.

Fig. 3. Rudimentary hypodermal bundle and cluster of hypodermal sclereids (arrow). P2313 Btop # 0. X 370.

Fig. 4. Central part of petiole showing inverse orientation of vascular tissue between six bundles of median arc and three bundles of adaxial arc. Arrows indicate protoxylem lacunae. P2313 Btop # 0. X 111.

Fig. 5. Small peripheral bundle from abaxial series (III) and surrounding fibrous sheath. Arrows indicate probable tannin cells. P2313 Btop # 0. X 430.

Fig. 6. Vascular bundle from abaxial arc below median arc showing protoxylem lacuna, branched transverse vein (arrow) and sclerenchymatous cells sheathing protoxylem lacuna and phloem. P2313 Btop # 0. X 430.

Fig. 7. Vascular bundle from median arc showing darkened protoxylem lacuna, distinct ring of surrounding thin-walled cells, thin-walled metaxylem elements, phloem cells, and reduced fibrous sheath. Note tylose-like structure in metaxylem and probable tannin cells (arrows). P2313 Btop # 0. X 430.

Fig. 8. Longitudinal section through vascular bundle in Fig. 7 showing remains of protoxylem elements, thickened walls of cells surrounding protoxylem lacuna, and thin-walled metaxylem element with tylose. P2313 Btop side # 0. X 415.

Fig. 9. Detail of possible metaxylem elements with helical secondary wall thickenings. P2313 Btop side # 0. X 770.

Fig. 10. Longitudinal section through phloem. Note transverse to slightly oblique end walls and tannin cell (arrow). P2313 Btop side # 0. X 540.

f = fibers, m = metaxylem, ph = phloem, pl = protoxylem lacuna, pr = protoxylem, ps = parenchyma sheath, r = rib, ty = tylose.

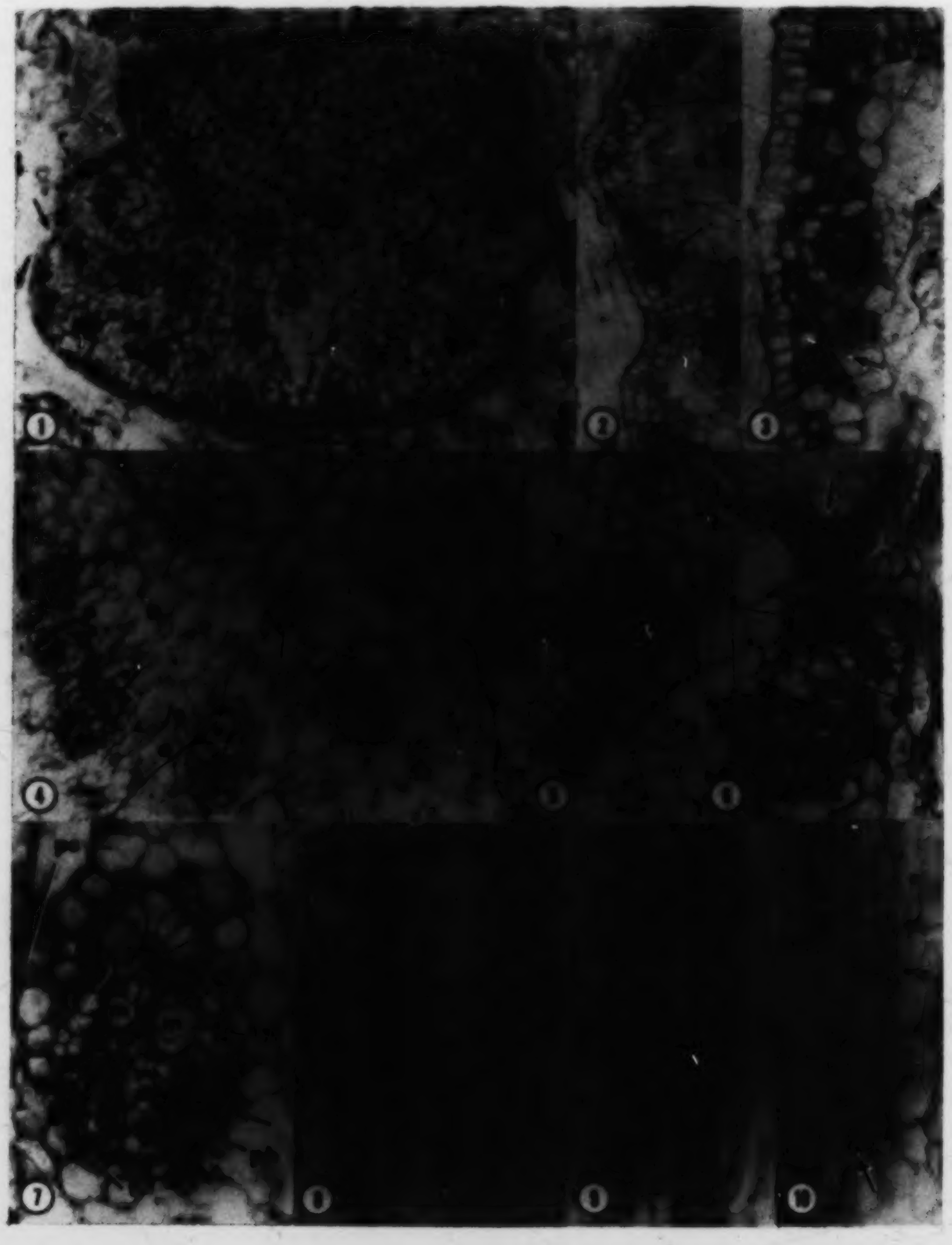
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Plate II, 2

Heleophyton helobioides gen. et sp. nov. petiole.

Fig. 11. Aerenchymatous ground tissue showing lacunae delimited by uniseriate partitions of thin-walled parenchyma. Note probable tannin cells (arrows). P2313 Btop # 0. X 190.

Fig. 12. Diaphragm-like structure traversing lacuna in ground tissue. P2313 Btop # 0. X 375.

Fig. 13. Tannin cells in periphery of petiole. P2313 Btop # 1. X 300. 14. Partition composed of thick-walled cells with simple pits. P2313 Btop # 0. X 460.

Fig. 15. Transverse vein or rudimentary bundle in oblique cross section with faint bar-like thickenings on lateral walls. P2313 Btop # 0. X 540.

Fig. 16. Transverse section showing four transverse veins extending from vascular bundles. P2313 Btop # 4. X 85.

Fig. 17. Transverse section showing thin-walled, radially elongated epidermal cells and thick-walled, pitted cells of two-layered hypodermis. P2313 Btop # 0. X 480.

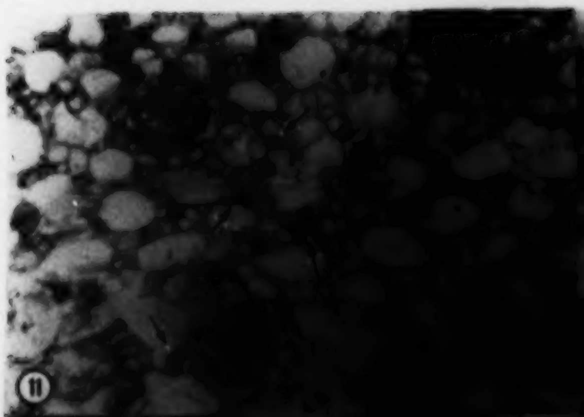
Fig. 18. Longitudinal section showing general cell shape of epidermis and axial discontinuity of thick-walled hypodermis. P2313 Btop side # 0. X 350.

Fig. 19. Transverse section showing thick-walled epidermal cells. P2313 Btop # 0. X 250.

Fig. 20. Transverse section of epidermis showing sinuous radial walls and thickened outer tangential walls. P2313 Btop # 1 X 770.

Fig. 21. Hypodermal sclereids. P2313 Btop # 0. X 430.

d = diaphragm, f = fibers, m = metaxylem, ph = phloem, pl = protoxylem lacuna, pr = protoxylem, ps = parenchymatous sheath, ty = tylose.



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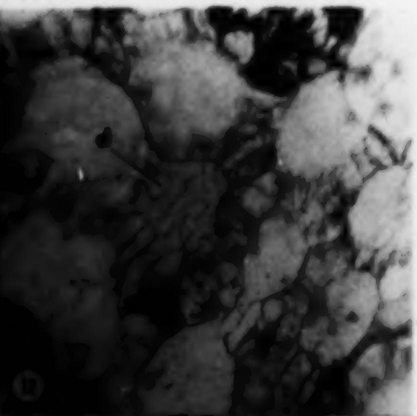

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Plate II, 3

Transverse sections of petioles showing vascular bundle distribution.

Fig. 22. *Sagittaria montevidensis* (modified from Meyer 1932, 1935).

Fig. 23. *Echinodorus macrophyllus* (modified from Meyer 1932, 1935).

Fig. 24. *Heleophyton helobioides*. X 430.

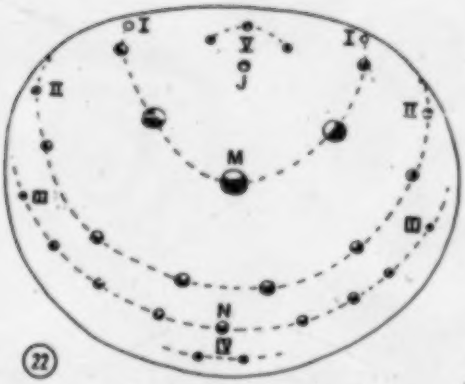
Fig. 25. *Echinodorus cordifolius*. X 85.

Fig. 26. *Heleophyton helobioides*. X 430.

Fig. 27. *Nymphaea tuberosa* (redrawn from Conard 1905).

Fig. 28. *Butomus umbellatus* (redrawn from Cheadle and Uhl 1948). X 430.

m = metaxylem, ph = phloem, pl = protoxylem lacuna. white = protoxylem lacuna, black = metaxylem and phloem, peripheral circles = hypodermal bundles.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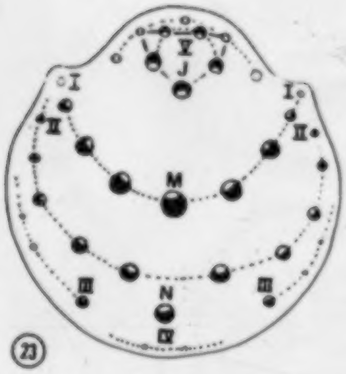
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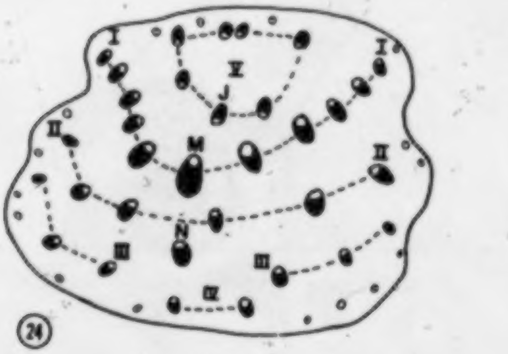
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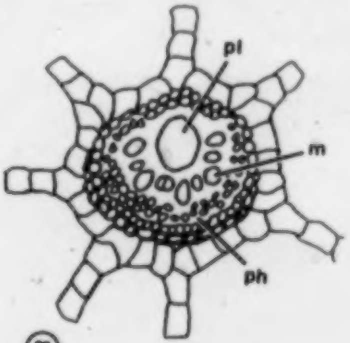
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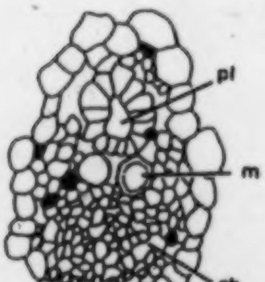
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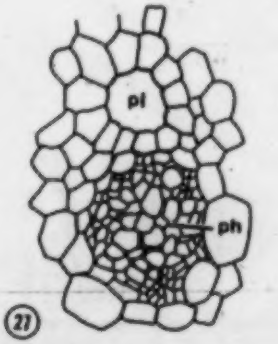
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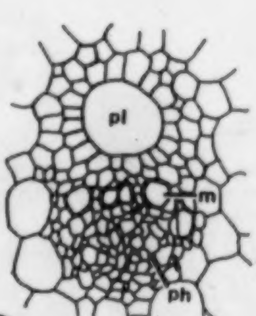
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Chapter 3: Permineralized monocotyledons from the Middle Eocene Princeton chert (Allenby Formation) of British Columbia: Arecaceae.*

Introduction

Angiosperms are among the most common plant remains found in the Middle Eocene Princeton chert from southern British Columbia, Canada. Based largely on studies since the mid-1980's, a diverse assemblage of both dicotyledonous and monocotyledonous vegetative and reproductive organs have been identified. Extant dicot families represented include: Rosaceae (BASINGER, 1976a, b; CEVALLOS-FERRIZ & STOCKEY, 1990a, b), Lythraceae (CEVALLOS-FERRIZ & STOCKEY, 1988a), Nymphaeaceae (CEVALLOS-FERRIZ & STOCKEY, 1989), Magnoliaceae (CEVALLOS-FERRIZ & STOCKEY, 1990c), Vitaceae (CEVALLOS-FERRIZ & STOCKEY, 1990d), and Sapindaceae (ERWIN & STOCKEY, 1990a). Although less abundant, monocotyledonous remains include a petiole of Alismataceae (ERWIN & STOCKEY, 1989), rhizomes of Liliales (ERWIN & STOCKEY, 1990b, c), the vegetative body of a small plant related to Cyperaceae or Juncaceae, (ERWIN & STOCKEY, 1990d), araceous seeds (CEVALLOS-FERRIZ & STOCKEY, 1988b), and vegetative organs of a coryphoid palm (BASINGER, 1976a; BASINGER & ROTHWELL, 1977; ERWIN, 1987; ERWIN & STOCKEY, 1990c).

In a general survey of the Princeton chert plants, BASINGER (1976a) briefly described isolated palm petioles, midribs, and roots. Petiole and midrib structure was found to be most similar to the fan-leaved coryphoid group; however, because petioles and midribs provide only taxonomically significant characters for relationship to a major group (TOMLINSON, 1961) assignment of these remains to a specific subfamily was not possible at the time (BASINGER, 1976a).

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*A version of this chapter has been submitted to Palaeontographica B.

This paper represents a renewed investigation of the Princeton palm remains. Stems with attached petiole bases and roots, midribs with attached laminae, and associated petioles, midribs, and laminae are described. A new taxon Uhlia allenbyensis gen. et. sp. nov. is proposed for the Princeton stems, petioles, and roots and assigned to the subfamily Coryphoideae. Comparison to modern palms shows that the fossil material shares several features with three genera: Rhapidophyllum, Brahea, and Serenoa.

Materials and methods

The vegetative palm remains examined in this study are preserved as siliceous permineralizations in chert blocks collected from the Princeton chert locality. This locality occurs in the Allenby Formation, Princeton Group (BONEHAM 1968) and is characterized by a 10 m thick section of 49 layers of interbedded chert and coal with an occasional thin ash bed (STOCKEY 1984). A Middle Eocene age has been reported for the Allenby Formation based on K-Ar dates from volcanic rocks within the formation (ROUSE & MATHEWS 1961; MATHEWS 1964; HILLS & BAADSGAARD 1967), palynological correlations (ROUSE et al. 1971; MATHEWS & ROUSE 1984), and studies of fossil insects and freshwater fishes (WILSON 1977a, b, 1978, 1980, 1982, 1988).

Fossil specimens were studied using the cellulose acetate peel technique (JOY et al. 1956) modified by the use of hydrofluoric acid (BASINGER & ROTHWELL 1977; BASINGER 1981). Peel sections were mounted on microscope slides with Eukitt or Coverbond xylene soluble mounting medium for microscopic examination.

Material of Rhapidophyllum hystrix (FTG #63-427 & 63-428), Serenoa repens (FTG # P-244B), and two species of Brahea, B. berlanderi Bartlet (HG #28812, Boutin 3376) and B. decumbens Rzedowski (HG #35650) was prepared for light microscopy using standard paraffin embedding techniques (JOHANSEN, 1940). Dried material was rehydrated by boiling in a mixture of water and household bleach for several minutes (TOMLINSON, 1961), then fixed in 50% FAA (formalin, acetic acid, and alcohol), dehydrated in an alcohol series, and embedded in paraffin (Paraplast Plus). Ten to twelve micron sections were cut using a rotary microtome, mounted on microscope slides, and stained with safranin and fast green. All slides are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Results and Descriptions

Systematic section

Family: Arecaceae Schultz-Schultzenstein
Subfamily: Coryphoideae Griffith
Tribe: Corypheae Martius
Genus: Uhlia gen. nov. Erwin & Stockey
Species: Uhlia allenbyensis sp. nov. Erwin & Stockey

Occurrence: Allenby Formation, Middle Eocene, Princeton chert locality, Princeton, British Columbia, Canada.

Diagnosis: Stems with attached sheathing petiole bases and roots. etagen-meristem (phellogen) forming narrow periderm-like outer layer. Central cylinder without peripheral sclerotic zone. Central vascular bundles circular to oval in cross section, 0.38 - 0.67 mm radially X 0.24 - 0.40 mm tangentially; xylem sheathed by parenchyma; containing mostly two wide metaxylem vessels. Metaxylem vessels, 85 - 150 um wide, (mean = 120 um); intervascular pitting scalariform; perforation plates mostly simple; occasionally with 2 - 4 bars on slightly oblique end walls. Phloem one strand, sheathed by semicircular-shaped fibrous cap. Ground tissue parenchymatous; localized areas aerenchymatous; central ground tissue including fibrous strands, 24 - 73 um in diameter. Peripheral fibers of phloem cap and strands with longitudinal files of stegmata. Stegmata spherical, druse-like, 11 - 18 um wide.

Petioles unarmed, (?) split at base in midregion, with remnants of hairs. Hairs with multicellular base of irregular, thick-walled cells. Central vascular bundles in cross section, 0.32 - 0.51 mm radially X 0.22 - 0.41 tangentially, with mostly 1 wide metaxylem vessel, 60 - 85 um wide. Vessels with scalariform lateral wall pitting, perforation plates scalariform, very oblique with 10 - 15 bars. Phloem 1 - 2 strands; width and prominence of partition variable, often inconspicuous or weakly developed. Bundle sheath fibrous, interrupted at level of metaxylem by thin or thick-walled parenchyma. Ground tissue parenchymatous, lacunose; lacunae in cross section variable in size, separated by narrow, transversely elongated irregularly-lobed cells; including scattered fibrous strands, 20 - 70 um in diameter.

Roots attached to one side of stem; 4.0 - 10.0 mm wide; stele medullated; polyarch; medullary vessels present. Wide metaxylem vessels, 60 - 370 um in diam.; lateral wall pitting scalariform; perforation plates simple. Pericycle 1 - 3 cells wide. Endodermis one layer, cells with U-shaped thickenings. Outer cortex 3-layered; cells of outer and inner layers thin-walled; middle layer fibrous; including numerous cells with dark contents. Middle cortex lacunose; lacunae radially-extended, delimited by parenchymatous, chain-like partitions, including scattered, isodiametric cells with dark contents. Inner cortex with 3 - 4 layers of radially aligned cells, including peripheral circular to oval-shaped, thick-walled sclereids. Cortical fibrous strands and mucilage canals absent.

Holotype - P1351 A-C (Plate 1, Fig. 1)

Paratypes - Stems: P1335A-D; P1351A-C; P1387A-E; P1390; P1397A-F

Petioles: P1118C Top; P1123H Bot; P1124C Bot, D Bot, G; P1171A&B; P1197; P1274A2; P1390G3.

Roots: P1123K Top; P1124E Bot, F Top, G Top; P1197B Bot; P1203C Top; P1205D Top; P1282S Top; P1349E Bot; P1379B Bot; P1387D Top; P1789A, B Top, C Bot, K1 Top.

Etymology: Genus named for Dr. Natalie W. Uhl for her contributions to our knowledge of extant palms. The specific epithet refers to the abandoned mining town of Allenby, for which the Middle Eocene Allenby Formation is named.

Anatomical Description

Stems:

Five stem fragments with attached roots and remnants of sheathing petiole bases have been found in five separate chert blocks (Pl. III, 1

Fig. 1, Pl. III, 2 Fig. 1). The holotype specimen (P1351A-C; Pl. III, 1 Fig. 1) is about 9 cm wide; however, only about one-half of the original stem is represented. All five specimens are morphologically and anatomically the same suggesting that they represent only one type of stem. Common to all are roots attached to one side and remnants of petioles on the other (Pl. III, 1 Fig. 1; Pl. III, 2 Fig. 1). Surrounding each stem is a narrow periderm-like layer (Pl. III, 2 Fig. 1, arrows; Pl. III, 3 Fig. 13) composed of rectangular to irregularly shaped cells in radial files. Many cells of this layer are thick-walled and filled with dark contents (Pl. III, 3 Fig. 13).

The stems in cross section show three regions based on their relative position, differences in bundle morphology and number, and characteristics of the ground tissue. These zones are most distinct on the sides of the stems bearing petioles. Within the outermost zone, there are leaf traces and smaller, widely-spaced vascular bundles (Pl. III, 1 Fig. 1 at a, 5). At the periphery of this zone, leaf traces are cut longitudinally and appear as dark lines that extend across the outer half of the zone (Pl. III, 1 Fig. 1). Ground parenchyma is compact with few intercellular spaces and includes numerous small fibrous strands (Pl. III, 1 Fig. 5). Most cells in this region are isodiametric, but others are tangentially elongated.

Internal to the outermost zone is a narrow region with numerous small, closely-spaced vascular bundles (Pl. III, 1 Fig. 1 at b, 6). Each bundle shows a C-shaped fibrous bundle cap at the phloem pole, occasionally a single wide metaxylem vessel, and narrow protoxylem elements. The ground tissue is like that in zone "a"; but fibrous strands are less frequent (Pl. III, 1 Fig. 6).

The central region extends from the inner boundary of "b" to the center of the stem (Pl. III, 1 Fig. 1 at c). At the periphery and scattered throughout the stem center are incipient leaf traces and small axial bundles (Pl. III, 1 Fig. 2) in various stages of leaf trace development (Pl. III, 1 Figs. 7-9). Traces representing possible inflorescence axes or lateral branches occur at the periphery of this zone (Pl. III, 1 Fig. 10). These traces show one large leaf trace surrounded by a halo of ca. 12 smaller satellite bundles (Pl. III, 1 Fig. 10). Peripheral bundles are more abundant and have bundle caps directed away from the stem center, whereas bundles toward the center are less numerous and randomly oriented. Localized areas of relatively large air spaces delimited by a network of parenchyma cells, 1 - 2 cells wide, are found in the periphery and stem center (Pl. III, 1 Figs. 4, 8). Scattered throughout the ground tissue are small fibrous strands, 24 - 73 um wide (Pl. III, 1 Figs. 3, 4).

The central vascular bundles are circular to oval in cross section and 0.24 - 0.40 mm tangentially X 0.38 - 0.67 mm radially (Pl. III, 1 Fig. 2). Phloem consists of an oval to elliptical strand capped by a fibrous, semicircular to crescentiform sheath (Pl. III, 1 Figs. 2, 5-7). Fibers are narrow, septate (Pl. III, 1 Fig. 12), and those in the outermost layer of the cap show longitudinal files of spherical druse-like stegmata, 11 - 18 um in diameter (Pl. III, 1 Fig. 13). Stegmata are also found associated with peripheral fibers of the fibrous strands (Pl. III, 1 Fig. 3, arrow).

The xylem consists of 1 - 6 wide metaxylem vessels and is sheathed by parenchyma (Pl. III, 1 Figs. 2, 7, 9). Variation in vessel number relates to different stages of leaf trace formation. For example, bundles with one or two wide vessels and little or no protoxylem are referred to as axial bundles (Pl. III, 1 Figs. 2, 7) (ZIMMERMANN & TOMLINSON 1965, 1971; ZIMMERMANN & SPERRY 1983; TOMLINSON, 1984). Axial bundles as traced acropetally show an increase in the number of protoxylem and metaxylem elements. In the fossil, vascular bundles display 4 - 6 wide vessels prior to their departure into the leaf base (Pl. III, 1 Figs. 7-9). Once the metaxylem of the axial bundles separates from the larger trace (Pl. III, 1 Figs. 8, 9), the larger trace is then referred to as a leaf trace (ZIMMERMANN & SPERRY 1983) and consists of protoxylem and phloem only (Pl. III, 1 Figs. 5, 9).

Metaxylem vessels range from 85 to 150 um in diameter with a mean width of 120 um. Vessel members in longitudinal section are short ranging from 240 - 460 um long, have scalariform to reticulate intervascular pitting (Pl. III, 1 Figs. 11, 15), and mostly simple perforations on slightly oblique end walls (Pl. III, 1 Fig. 14). Occasionally vessel members show scalariform perforation plates with 2 - 4 bars (Pl. III, 1 Fig. 15). Tyloses are abundant in the tracheary elements and are especially conspicuous in wide metaxylem vessels (Pl. III, 1 Figs. 2, 14, 16).

Petioles:

The isolated specimens examined show minor differences in petiole size and shape in cross section, vascular bundle size and morphology, and structure of the ground tissue. However, as shown below, many of these apparent differences between specimens are found within a single specimen or as an intergradation features among the specimens. Therefore, the observed variability most likely reflects non-comparable levels, age differences among specimens, section obliqueness, and/or the quality of preservation of the same type of petiole. In addition, the isolated specimens show histological features consistent with the attached petioles and are therefore included as paratypes. A small elliptical petiole and a larger fragment are described but not included as paratypes. This petiole type (referred to as "a") is different in several features from the attached petioles and is significant in having vascular bundle morphology identical to that found in the midribs and larger veins of the laminae.

Epidermis and Ground Tissue:

All stem fragments show remnants of sheathing, overlapping petiole bases that are at least 8 cm broad (Pl. III, 2 Fig. 1). In cross section, abaxial epidermal cells are cubical, some appear thick-walled, and many are filled with dark contents (Pl. III, 3 Figs. 9, 11). One larger fragment shows remnants of a multicellular hair composed of irregularly-shaped thick-walled, pitted cells in the abaxial epidermis. These hairs resemble those of the midribs (Pl. III, 5, Fig. 5). Internal to the abaxial epidermis is a narrow zone of compact, mostly thin-walled polygonal cells several layers deep (Pl. III, 3 Fig. 9). These cells are larger than the epidermal cells, but generally smaller than the internal ground tissue (Pl. III, 3 Fig. 9). In some specimens, cells within this region are thick-walled and have dark contents (Pl. III, 3 Figs. 10, 11). This narrow zone would correspond to that region described as "chlorenchyma" in extant palms (TOMLINSON, 1961).

Just internal to the "chlorenchyma," the ground tissue consists of compact, thin-walled cells. Some areas within this peripheral ground tissue show cells that appear to have undergone periclinal divisions forming a periderm-like layer of radial files of square to irregularly-shaped cells (Pl. III, 3 Fig. 9). In larger isolated petiole fragments, this periderm-like layer is very extensive and consists of square to rectangular, thin-walled cells in the outer layers and thicker-walled cells internally (Pl. III, 3 Fig. 12). The thicker-walled cells are filled with dark contents (Pl. III., 3 Fig. 12). A similar periderm-like layer surrounds the stems (Pl. III, 3 Fig. 13).

Embedded within the peripheral ground tissue are two to three series of fibrous strands (Pl. III, 3 Figs. 1 - 3, 9). Strands of the outermost series are the smallest, while those in the inner series are larger (Pl. III, 3 Figs. 1 - 3, 9). Peripheral vascular bundles are the smallest but grade into a series of larger bundles with massive fibrous phloem sheaths (Pl. III, 3 Figs. 1, 2). The abaxial bundles are oriented parallel to one another with their phloem sheaths directed toward the abaxial epidermis (Pl. III, 2 Fig. 2; Pl. III, 3 Fig. 1 - 3). Radial extent of the phloem sheath decreases in bundles toward the center of the petiole (Pl. III, 3 Fig. 8). The peripheral bundles are more congested than those toward the center of the petiole, but are not confluent (Pl. III, 3 Figs. 1 - 3).

The peripheral ground tissue consists of relatively compact, isodiametric cells and becomes more aerenchymatous toward the central region of the petiole (Pl. III, 3 Figs. 2, 3, 5). Occasionally the ground tissue cells adjacent to peripheral vascular bundles are tangentially elongated. Central ground tissue shows numerous lacunae delimited by partitions of transversely elongated cells (Pl. III, 3 Fig. 5). In longitudinal and oblique sections, cells of the partitions form chains 4 - 10 cells long (Pl. III, 2 Fig. 10; Pl. III, 3 Fig. 3). In some specimens, the cells have collapsed or are poorly preserved (Pl. III, 2, Fig. 6; Pl. III, 3 Figs. 4, 7). Poor preservation may be due to the abundant fungal hyphae that fill cells of the ground tissue and bundle sheaths (Pl. III, 3 Figs. 3, 7, 14). Fibrous strands, 24 - 73 um wide, are scattered throughout the ground tissue (Pl. III, 2 Figs. 2, 6, 9, 10; Pl. III, 3 Figs. 2, 3, 5, 6).

The adaxial epidermis in cross section is a single layer of cubical thick-walled cells, many of which are filled with dark contents (Pl. III, 3 Fig. 12). A wide peripheral zone consists of a mixture of compact isodiametric to irregularly-shaped, thin- and thick-walled cells (Pl. III, 3 Fig. 4). These cells resemble those of the adjacent thinner-walled ground tissue but are generally smaller. The thick-walled cells have dark contents (Pl. III, 3 Fig. 4). Peripheral adaxial bundles lack massive fibrous phloem sheaths and are randomly oriented (Pl. III, 3 Figs. 4, 6). Fibrous strands of variable size are abundant and occur in 2-6 series at the periphery (Pl. III, 3 Figs. 1, 4). Generally, the smallest strands occur in or adjacent to the subepidermal layers (Pl. III, 3 Fig. 4).

Vascular Tissues:

Vascular bundles are evenly-distributed throughout the parenchymatous ground tissue (Pl. III, 2 Figs. 2-4; Pl. III, 3 Fig. 2). Central vascular bundles in the petiole base show mostly one wide metaxylem vessel, several narrow protoxylem elements and one or two phloem strands (Pl. III, 2 Fig. 8). All but the smallest vascular bundles have both xylem and phloem sheathed by fibers. Fiber sheaths of the central vascular bundles are crescentiform in cross section, nearly equal in width (Pl. III, 3 Figs. 3-8), and interrupted at the level of the wide metaxylem vessels by thin- or thick-walled parenchyma (Pl. III, 3 Figs. 3-8). Phloem sheaths are massive in bundles located along the abaxial surface (Pl. III, 2 Fig. 2; Pl. III, 3 Figs. 1, 3).

As in the attached petioles, most isolated specimens appear to show vascular bundles with a single phloem strand (Pl. III, 2 Fig. 9); however, there is variation among the specimens with regard to this character. Several of the larger fragments have both bundles with the phloem undivided (Pl. III, 3 Fig. 5) and bundles with two phloem strands separated by a median partition (Pl. III, 2 Fig. 11; Pl. III, 3 Fig. 6). In still others, phloem in nearly all the larger bundles have two distinct strands (Pl. III, 2 Figs. 6, 7; Pl. III, 3 Figs. 7, 8). Aside from differences in the prominence of the median partition, overall bundle morphology and structure of the ground tissue is comparable among all specimens.

The number of metaxylem vessels varies from mostly one in the central bundles, but occasionally 2 or even 3 in other bundles. Wide metaxylem vessels range from 60 um to 150 um, the diameters vary relative to the size of the specimen. For example, wide metaxylem vessels in the small petiole illustrated in Plate III, 2, Figure 4 range from 60 - 85 um in diameter, whereas the wide vessels in the central bundles of a larger specimen range from 73-150 um wide. Protoxylem elements are narrower and 0.20 - 0.50 um wide. In longitudinal section, vessel members show scalariform intervascular pitting and scalariform perforation plates on very oblique end walls (Pl. III, 2 Fig. 13). Tyloses are frequent in the wide metaxylem vessels (Pl. III, 3 Figs. 4, 6, 8).

Phloem includes sieve tube members with elliptical sieve areas on the lateral walls (Pl. III, 2 Fig. 12). Most bundles show only a single phloem strand (Pl. III, 1 Fig. 8); however, an attached fragment shows at least one bundle that appears to have two phloem strands separated by a median fibrous partition (Pl. III, 3 Fig. 8, arrow).

Petiole type "a" (P1324 & P1384)—A small, oval to elliptical-shaped petiole (Pl. III, 2 Fig. 5) and a larger fragment shows differences in bundle morphology and ground tissue to those described above. This specimen has congested vascular bundles near the periphery, but bundles are fewer and become less crowded toward the petiole center. In cross section, the bundles differ in having one central wide metaxylem vessel flanked on either side by one or more narrow vessels (Pl. III, 2 Fig. 7). The fibrous sheath is interrupted at the level of the wide metaxylem vessels by thick-walled parenchyma (Pl. III, 2 Fig. 7) and most large bundles display two distinct phloem strands separated by a median sclerotic partition (Pl. III, 2 Fig. 7). Ground tissue differs from the other specimens in being more compact with small intercellular spaces and in having fewer fibrous strands (Pl. III, 2 Fig. 7). A thick cuticle covers the epidermis.

Multicellular hair bases or peltate scales similar to those found on the other petiole are found slightly sunken in the epidermis (Pl. III, 2 Fig. 14). Bundle morphology in this specimen is identical to that in the central bundles of the midribs and laminae (Pl. III, 4 Figs. 3, 4, 5, 7).

Roots:

Roots of Uhlia allenbyensis are 4 - 10 mm wide. The stele is 1 - 5 mm wide, medullated, cylindrical and polyarch with abundant protoxylem poles (Pl. III, 4 Figs. 1 - 4). Metaxylem vessels are widest near the pith and decrease in diameter toward the endodermis (Pl. III, 4 Figs. 1 - 4). The vessels range from 60 to 370 um in diameter. In longitudinal section they show scalariform to reticulate intervascular pitting and simple perforation plates. Roots near the level of insertion on the stem, show tracheary elements arranged in radial series but vessels are remote from one another (Pl. III, 4 Fig. 2) whereas in other specimens the tracheary elements form distinct radial files with little or no space between cells (Pl. III, 4 Fig. 4). At the level of root insertion, several wide vessels extend into the pith (Pl. III, 4 Fig. 2). Presence of medullary vessels in some isolated specimens is uncertain since the pith is poorly preserved (Pl. III, 4 Figs. 3, 4). Phloem strands are circular to radially-extended and alternate with the xylem (Pl. III, 4 Fig. 4). The endodermis is uniseriate and consists of U-shaped cells with thick radial and inner tangential walls. The pericycle is 1 - 2 cells wide (Pl. III, 4 Fig. 4). Vascular tissues are embedded in a zone of thick-walled cells (Pl.

III, 4 Figs. 3, 4).

The cortex shows three zones. A narrow inner cortex of compact, radially arranged small thin-walled cells surrounds the endodermis (Pl. III, 4 Fig. 3). Larger thick-walled pitted cells and cells with dark contents occur scattered around the inner cortex (Pl. III, 4 Figs. 2, 3). The middle cortex is aerenchymatous and consists of radially-extended lacunae separated by thin-walled partitions (Pl. III, 4 Fig. 3). Included in the partitions are small diameter cells with dark contents (Pl. III, 4 Figs. 2, 3).

Associated vegetative remains:

Midribs: (P1101D Top; P1123C Bot; P1171B2 Bot, C1&2 Top; D Top; P1263B Bot, C Top; P1282M Top; P1277B Bot, F side 2, G3 Bot; P1345D Bot; P1349E Bot; P1360D Top; P1384C Bot, D1 Bot; P1387D Top, E2; P1789I Top; L1)

Midribs with attached laminae are abundant and found associated with the petioles and stems, but have not been found attached to the petioles. Although midribs vary in size, shape, and the number of vascular bundles each contains, all show comparable internal anatomy and organization. Both adaxial (Pl. III, 5 Figs. 2, 3) and abaxial ribs (Pl. III, 5 Figs. 1, 4) are present. The largest ribs are adaxial and most likely represent a proximal level near the base of the lamina (Pl. III, 5 Figs. 2, 3). Midribs are square to rectangular in cross section, one to 3 mm long and about one mm wide, and include one to ten or more, centrally located vascular bundles (Pl. III, 5 Figs. 1 - 4). Epidermal and hypodermal layers are differentiated as in the laminae.

Multicellular hairbases composed of thick-walled cells with simple pits and filamentous thin-walled cells attached distally occur in the epidermis (Pl. III, 5 Fig. 5). Central ground tissue consists of compact parenchyma that occasionally includes cells filled with dark contents. Located opposite each rib is a single band of thin-walled expansion tissue that includes fibrous strands (Pl. III, 5 Fig. 2).

Central vascular bundles within the ribs are either completely separate (Pl. III, 5 Fig. 4) or all or several are joined by their fibrous sheaths (Pl. III, 5 Figs. 1-3). Large vascular bundles contain 3-5 wide metaxylem elements, several narrow protoxylem elements, and the phloem is divided into two strands by a central sclerotic partition (Pl. III, 5 Figs. 1-4). Most bundles appear to have a complete fibrous sheath, however, the sheath is interrupted at the level of the metaxylem by sclerotic parenchyma showing simple pits.

Laminae: (P1123C Bot; P1171B Bot, C Top; P1263B Bot, C Top; P1277B Bot, G3 Bot; F side 2; P1345B Bot, C Top; P1349E Bot; P1384D Bot; P1387D Top, E2; P1389I Top, K1 Bot, L1; P1390G)

Laminae are dorsiventral. In cross section, many show an adaxial palisade layer 2-4 cells high composed of compact, small vertically elongated, rectangular cells (Pl. III, 5 Figs. 6, 8); however, this layer is not always distinct (Pl. III, 5 Fig. 8). Cells of the central and abaxial mesophyll, on the other hand are larger, isodiametric, and more loosely-packed (Pl. III, 5 Figs. 6, 8). Abaxial epidermal cells in cross section are small, cubical, fairly uniform in size and have thick radial and inner tangential walls whereas adaxial epidermal cells are larger and deeper (Pl. III, 5 Figs. 6, 8). In surface view, the abaxial cells are narrow, rectangular, and longitudinally-extended (Pl. III, 4 Fig. 10). Anticlinal walls are straight (Pl. III, 5 Fig. 10). A thick cuticle covers the adaxial epidermis (Pl. III, 5 Fig. 6) whereas the abaxial surface of most laminae are infected with an epiphytic, perithecia forming fungus (Pl. III, 5 Fig. 1, arrows; 15). Most stomata are restricted to abaxial intercostal regions (Pl. III, 5 Figs. 3, 6, 12) and are not arranged in distinct files (Pl. III, 5 Fig. 9). Occasionally a few stomata lie above the larger veins (Pl. III, 5 Fig. 9, arrow). The guard cells in paradermal section are 24 - 27 um long and sunken to the level of the epidermis (Pl. III, 5 Figs. 6, 12). At each pole there are one to two rectangular terminal subsidiary cells oriented with their long axis perpendicular to the guard cells (Pl. III, 5 Fig. 10). The two terminal cells adjacent to guard cells are wider than the epidermal cells. Four L-shaped cells surround each substomatal chamber (Pl. III, 5 Fig. 11).

The hypodermis consists of subrectangular, tangentially-elongated cells in one layer below each surface (Pl. III, 5 Fig. 8). Circular-shaped fibrous strands are found adjacent to each hypodermis (Pl. III, 5 Figs. 6-8). Generally, the abaxial strands are larger and less abundant than those attached to the adaxial hypodermis (Pl. III, 5 Figs. 6-8). Small isolated strands sometimes occur in the adaxial or abaxial mesophyll.

The veins are nearly equidistant from each surface and not attached to the hypodermis by fibrous buttresses (Pl. III, 5 Figs. 6-8) although occasionally the adaxial pole of the fiber sheath of some veins is wider and more vertically extended toward the adaxial hypodermis. Larger veins resemble those of the midribs in that they show 1-3 wide tracheary elements and phloem divided into two strands by a median sclerotic partition (Pl. III, 5 Fig. 7). Large veins are surrounded by an indistinct outer parenchymatous sheath and an inner sclerenchyma sheath that is interrupted at the level of the wide metaxylem elements by thick-walled parenchyma (Pl. III, 5 Fig. 8, arrow). Smaller veins show a complete outer sheath or the sheath is discontinuous and completed adaxially by thick-walled parenchyma.

Comparison to Extant Palms

In his survey of vegetative palm anatomy, TOMLINSON (1961) found midrib anatomy to be important for separating the major groups of palms with induplicate fan leaves from those with reduplicate pinnate leaves. At the generic rank, laminae provide the most significant diagnostic characters because this part of the plant shows the most variation (TOMLINSON, 1961). Petioles, stems, and roots on the other hand, are more anatomically uniform, but do provide a few diagnostic characters. Among these are the presence of fibrous strands in the central ground tissue of the stem (TOMLINSON, 1961), number of wide metaxylem vessels and phloem strands in the central bundles of the stems and petioles (TOMLINSON, 1961; KLOTZ, 1977, 1978a, b), and the presence of cortical fibrous strands in the roots (TOMLINSON, 1961).

Stems of Uhlia have fibrous strands in the central ground tissue. This character has been reported in 8 extant non-coryphoid genera and only two coryphoid palms (TOMLINSON, 1961). Since the midribs and laminae are not found attached, Uhlia is compared to both the non-coryphoid (Tables III, 2, 3) and coryphoid genera (Tables III, 4, 5). Information regarding lamina, midrib, and petiole characters for these genera is provided for further comparison with the fossil material. Table III, 1 lists the 31 genera currently recognized in the tribe Corypheae, subfamily Coryphoideae. A summary of leaf characters for the coryphoid genera that have petiolar vascular bundles with one wide metaxylem vessel and two phloem strands, but lack fibrous strands in the central ground tissue of the stem is provided in Tables III, 6 and 7.

Non-coryphoid palms:

Pinanga Blume differs from Uhlia in having only one wide metaxylem vessel in the central vascular bundles of the stem, whereas there are two in the central bundles of Uhlia. Pinanga also differs from Uhlia with respect to petiole and root anatomy. Petioles of Pinanga have hairs that differ from Uhlia and the xylem sheath is parenchymatous. Roots of Pinanga contain abundant fibers in the outer cortex and irregular fibrous strands scattered within the parenchymatous partitions of the inner cortex (TOMLINSON, 1961). The inner cortex of the fossil roots is lacunose, but cortical fibrous strands are absent. Metaxylem in Pinanga forms inverted V-shaped strands that overarch or enclose individual phloem strands (TOMLINSON, 1961). This feature has not been seen in the roots of Uhlia.

Salacca Reinwardt differs from Uhlia in having central bundles in the stem with mostly one wide metaxylem vessel and no periderm-like layer surrounding the stem (TOMLINSON, 1961). Petioles differ in that xylem of the vascular bundles is sheathed by parenchyma, peripheral vascular bundles are congested and the central bundles are arranged in a distinct median arc (TOMLINSON, 1961).

Central vascular bundles in the stems of Leopoldinia Martius show mostly one wide metaxylem vessel, but also two as in Uhlia. Petiole vascular bundles, however, show mostly two wide metaxylem vessels, whereas in Uhlia there is mostly one.

Bactris N.J. Jacquin ex Scopolli like Leopoldinia displays one wide metaxylem vessel, but has mostly two in the central vascular bundles of the stem. Bactris shows several characters not found in Uhlia. The stem epidermis of Bactris is covered with numerous hairs (TOMLINSON, 1961). Each one consists of a sclerotic base of thick-walled irregularly shaped thick-walled cells with filamentous thin-walled cells attached distally (TOMLINSON, 1961). Similar hairs are abundant on the petioles. In all specimens of Uhlia, the epidermis is not present and probably was sloughed off by the activity of the etagen-phellogen. In the petiole bundles of Bactris, xylem is sheathed by parenchyma. Thick-walled mucilage canals frequently occur in the cortex of the roots of this genus (TOMLINSON, 1961). Thick-walled cells do occur scattered throughout the inner cortex of Uhlia, but the exact nature of the cells is not known. Stegmata are common in the stem and leaf of Bactris, but are hat-shaped (TOMLINSON, 1961) whereas stegmata in Uhlia are spherical and druse-like.

Tracheary elements in the stem of Phytelephas Ruiz & Pavon vary from 2 or 6 - 12 in the same species (KLOTZ, 1977). Many of these elements are imperforate or with scalariform perforation plates that have numerous bars on very oblique end walls (KLOTZ, 1977). However, vessels with mostly simple perforation plates occur in the stem of Uhlia. Petioles of Phytelephas have central vascular bundles with two wide metaxylem vessels rather than one as in Uhlia. Xylem is sheathed by parenchyma in petiole bundles rather than fibers as in Uhlia (TOMLINSON, 1961). Mucilage canals are abundant in the cortex and pith of roots of Phytelephas (TOMLINSON, 1961), but these structures have not been positively identified in roots of Uhlia.

Wallichia differs from Uhlia in having numerous hairs on the petioles, xylem sheathed by parenchyma, petiole bundles with 1 - 2 wide vessels, and an undivided phloem strand (TOMLINSON, 1961; KLOTZ, 1977). Uniform, cylindrical, fibrous strands occur scattered throughout the lacunose cortex of the roots of Wallichia (TOMLINSON, 1961). Stegmata are hat-shaped (TOMLINSON, 1961) rather than spherical and druse-like as in Uhlia.

Cocos L. is similar to Uhlia in number of wide metaxylem vessels and phloem strands in the stems and petioles, but differs in having xylem sheathed by sclerotic parenchyma, ground tissue of the stem not expanded, roots with mucilage canals and steles that lack medullary vessels (TOMLINSON, 1961). In addition, mature stems of Cocos are tall and solitary (UHL & DRANSFIELD, 1987). The vessel elements are long, ca. 1200 - 1630 um long and 170 - 250 um wide (KLOTZ, 1977). Stems of Uhlia on the other hand are interpreted as rhizomatous or decumbent and have very short vessels 240 - 460 um long and 85 - 150 um wide.

Coryphoid palms:

The two remaining taxa with central fibrous strands are the fan-leaved coryphoid palms, Rhapidophyllum and Brahea. Rhapidophyllum includes the single species R. hystrix which is considered to be a relict genus endemic to the southern U.S.A. (SHUEY & WUNDERLIN, 1977; UHL & DRANSFIELD, 1987). This species has costapalmate leaves with unarmed petioles and a rhizomatous growth habit, but differs from the fossil in having stems covered with long, stout spines and central vascular bundles with 2 - 5 wide metaxylem vessels (KLOTZ, 1977).

Petioles of Rhapidophyllum show numerous, superficial wart-like hairs and central vascular bundles with 4 - 6 small diameter metaxylem vessels (Pl. III, 6 Fig. 1; Table III, 5), whereas the fossil petioles have mostly one wide metaxylem vessel. Hairs on the petioles of Uhlia differ from those of Rhapidophyllum in size, shape in longitudinal section, and position on the petiole surface (Pl. III, 2 Fig. 14).

Midribs of Rhapidophyllum differ from the fossil ribs in being most prominent abaxially and show one to several central bundles with very narrow tracheary elements surrounded by smaller peripheral vascular bundles; the lateral ones with fused phloem sheaths (Pl. III, 6 Fig. 3; Table III, 5).

Laminae, on the other hand, are similar to the fossil in being dorsiventral, having an adaxial palisade of several layers, a thick adaxial cuticle, diffuse arrangement of stomata restricted to the abaxial surface, in guard cell length, relative numbers of adaxial and abaxial fibrous strands, horizontally-elongated hypodermal cells in cross section, four L-shaped cells surrounding the substomatal chamber, and narrow, shallow elongate abaxial epidermal cells (Pl. III, 6 Figs. 6, 7, 10-12; Table III, 4). Laminae of Rhapidophyllum differ from the fossil laminae in having hairs (Pl. III, 6 Fig. 10), numerous anticlinally-extended adaxial fibrous strands (Pl. III, 6 Fig. 10), narrow and relatively few transverse veins (Pl. III, 6 Fig. 6), and narrow metaxylem vessels in veins of the midribs (Table III, 5) and laminae.

Uhlia also differs from Brahea. Central vascular bundles in stems of Brahea have a massive fiber sheath adjacent to a small phloem strand, a feature lacking in Uhlia. A rhizomatous species, B. decumbens, like the fossil has persistent sheathing leaf bases and lacks spines. Petioles of Brahea differ from Uhlia in having congested peripheral vascular bundles with confluent bundle sheaths, central bundles are wide, xylem is sheathed by parenchyma, and vascular bundles contain one central wide vessel flanked on either side by several narrower tracheary elements (TOMLINSON, 1961). Furthermore, laminae of Brahea differ from the fossil material with respect to guard cell length, number and shape of the cells surrounding the substomatal chamber, fiber strand size, shape, and distribution, and frequency and width of the transverse veins (Table III, 4).

Comparison of Uhlia to extant palms with central fibrous strands in the stems shows that the fossil differs in several features of stem, petiole, and root structure from these living genera. Based on the following combination of characters: stems with small central fibrous strands, central vascular bundles with two wide metaxylem vessels, petioles with one to two phloem strands, petiole hairs present, central bundles of petiole with mostly one wide metaxylem vessel, xylem and phloem of petioles sheathed by fibers, fibrous strands in ground tissue of petioles, etagen-meristem associated with stems and petioles, spherical and druse-like stegmata, mucilage canals absent in all organs, and roots with medullary vessels, a new taxon Uhlia allenbyensis is proposed for the vegetative body of the Princeton palm.

Comparison of petiole type "a" to extant coryphoid palms shows the fossil (Pl. III, 2 Figs. 5, 7) closely resembles the genus Serenoa (Pl. III, 6 Fig. 2), but differs mainly in hair morphology. Serenoa is a monotypic genus that includes the single species S. repens. Serenoa is considered to be closely related to Brahea (UHL & DRANSFIELD, 1987). Hairs were reported as absent by TOMLINSON (1961) but were found in the present investigation. Hairs or ramenta of Serenoa are sparse and occur in shallow depressions in the abaxial surface near each margin of the petiole (Pl. III, 6 Fig. 15). Each consists of a small, sunken base of narrow, thick-walled cells with a distal, anvil-shaped expanse of thin-walled cells (Pl. III, 6 Fig. 15). The base narrows at the point of attachment of the thin-walled cells (Pl. III, 6 Fig. 15).

Hairs in the fossil, however, have a wide base composed of irregular-shaped, thick-walled cells that flattens out distally (Pl. III, 2 Fig. 14). The large adaxial fossil midribs (Pl. III, 2 Figs. 2, 3) are also nearly identical to those in this genus (Pl. III, 6 Fig. 5). However, the laminae of Serenoa differ from the fossil in being isolateral, in having a palisade below each surface, in frequency and size of hypodermal fiber strands, the shape of hypodermal cells in cross section, and number and shape of the cells surrounding the substomatal chamber (Pl. III, 6 Figs. 13, 14, arrow). Stems of Serenoa are rhizomatous and clothed with persistent, sheathing leaf bases as in Uhlia, but lack central fibrous strands (TOMLINSON, 1961). Roots are also similar to Uhlia in showing medullary vessels.

Implications of petiole type "a", midribs, and laminae:

Although the midribs and laminae have not been found attached to the stems, the presence of only one type of these remains in the chert and their close association with the stems suggest they belong to the same taxon. TOMLINSON (1961) found that midrib structure could be used to distinguish induplicate fan-leaved palms from palms with reduplicate, pinnate leaves. Midribs of reduplicate leaves show central vascular bundles surrounded by a common fibrous cylinder and two bands of expansion tissue opposite the rib, whereas induplicate leaves show ribs with central bundles surrounded by smaller peripheral vascular bundles and fibrous strands. Located opposite the rib is a single band of expansion tissue. However, the distinction between the two types is not without exception. For example, leaves of a few palmate-leaved palms are reduplicate and show midrib structure like that found in pinnate leaves (Lepidocaryum Martius and Mauritia L.f.; TOMLINSON, 1961). More recently, UHL (1972) found that midribs of the induplicate, palmate leaves of Itaya H. E. Moore are structurally like reduplicate pinnate palms, but Itaya differs in having one band of expansion tissue rather than two. The induplicate pinnate leaves of the Caryotoid palms show reduplicate midrib structure (TOMLINSON, 1961). However, the presence of pinnate leaves with midrib structure like that in induplicate, fan-leaved palms has yet to be reported.

All the Princeton midribs examined show anatomy like induplicate, fan-leaved palms. The largest bundles display a shallow arc of 3 - 5 wide metaxylem elements, two phloem strands separated by a median sclerotic partition, and a fibrous bundle sheath interrupted at the level of the xylem by thick-walled parenchyma. In extant palms, midribs of this type are found only in the induplicate fan-leaved palms of the subfamily Coryphoideae sensu UHL and DRANSFIELD (1987) within the tribes Corypheae Martius, Borasseae Martius, and Sabalinae Martius (TOMLINSON 1961). Both the Borasseae and Sabalinae differ from the fossil with respect to structure of the laminae. Unlike the fossil laminae, the large vascular bundles in the borassoid palms are attached to one or both surfaces by fibrous buttresses, and hairs are common on the lamina. Sabal Adanson differs from the fossil in having isolateral laminae, veins in the adaxial mesophyll attached to each surface by fibrous buttresses, and veins with 3 separate strands of phloem (TOMLINSON, 1961).

Palm Habit

A rhizomatous growth habit is interpreted for Uhlia based on morphological and anatomical features of the stems. The occurrence of roots along one side of the stem and attachment of leaf bases to the other is suggestive of a rhizomatous habit. Certain aspects of stem anatomy are also consistent with this interpretation. TOMLINSON (1961) and KLOTZ (1977, 1978) have reported correlations between the diameter of the wide metaxylem vessels in the axial bundles from the central part of palm stems and growth habit. According to TOMLINSON (1961), the shortest and narrowest vessels are found in palms with short subterranean stems. In the fossil stems, vessels are also relatively short measuring between 240 - 460 um long. For example, vessels in the creeping stem of Salacca are only 400 - 520 um long. In a more recent study, KLOTZ (1978) also demonstrated that rhizomatous stems generally have narrow vessels, but that a size overlap does occur with species of erect-stemmed palms.

The eleven rhizomatous species studied by KLOTZ (1978) had a total range of vessel diameters of 0.03 - 0.18 mm, while the diameter of vessels of erect stems range from 0.04 - 0.45 mm and for scandent palms 0.07 - 0.46 mm. Wide metaxylem vessel diameters for Uhlia range from 0.085 - 0.150 mm with a mean 0.120 mm. Although the vessel diameters fall within the range of these three habit categories, the very short vessel lengths are most consistent with vessel lengths of rhizomatous species. With respect to the perforation plate, Uhlia is consistent with many rhizomatous species in having short sclariform perforation plates with only a few bars.

The presence of lacunose ground tissue in the petioles may provide further evidence for this growth habit. Aerenchyma is common in those palms inhabiting wet areas (RICH, 1987). Due to low growth stature, leaves and stems would be in contact with water of a marshy environment whereas taller more erect stems would probably not have petioles with well-developed aerenchyma. However, many palms that have sustained stem thickening produce large lacunae or air cavities between the expanding cells in the central ground tissue (RICH, 1987). The fossil stems could represent immature erect-stemmed palms. Palms remain quite low in stature for several years until the stem increases to a width nearly equal to the mature stem, then the stem increases in height. A stem may be several years old, but still very short (TOMLINSON, 1961).

Fossil Palms

The Arecaceae have an extensive fossil record dating back to the Cretaceous (DAGHLIAN, 1981; UHL & DRANSFIELD, 1987; CROSS et al., 1988). Tertiary palms are known from permineralized stems, petioles, laminae, and roots (e.g., KNOWLTON, 1888; STENZEL, 1904; TIDWELL et al., 1971, 1972, 1973; RAO & ACHUTHAN, 1971; SHEETE & KULKARNI, 1980); leaf compressions/impressions (NOE, 1936; LAMOTTE, 1952; READ & HICKEY, 1972; DAGHLIAN, 1978, 1981); fruits and seeds (REID & CHANDLER, 1933; CHANDLER, 1964; KOCH, 1972; COLLINSON, 1983a, b, 1987; DAGHLIAN, 1981; FRIIS, 1985); flowers (DAGHLIAN, 1981; SCAARSCHMIDT & WILDE, 1986); and pollen (MULLER, 1981). Unfortunately, this wealth of fossil material has yielded a distorted picture of palm diversity throughout the geologic record and has resulted in a muddled taxonomic framework for fossil palms.

Most descriptions of fossil palms are based on isolated vegetative and reproductive parts. Much confusion has stemmed from assigning these isolated remains to extant genera or organ genera, since such assignments often infer close relationships with modern counterparts that may not actually exist. For example, _Sabalites_ Saporta is an organ genus for fossil palm leaves that are costapalmate, like those of the extant genus, _Sabal_. However, costapalmate leaves are found in _Washingtonia_, _Coccothrinax_, _Rhapidophyllum_, and others. With the exception of Phoenix L., similarities in gross morphology of palm leaves makes it nearly impossible to assign living specimens of leaves to their respective genus, let alone classify fossil compressed leaves in an extant genus (READ & HICKEY, 1972). DAGHLIAN (1978) recently has shown the utility and importance of cuticular features, particularly stomatal organization, to recognize an extinct species of Sabal, S. dortchii DAGHLIAN, as well as two additional extinct coryphoid genera.

Further complications have resulted from new taxa being named that are indistinguishable from taxa already published or by grouping unrelated taxa into one genus (READ & HICKEY, 1972). ACHUTHAN (1967) described several fragments of putative permineralized palm laminae and a midrib as Palmophyllum dakshinense from the Deccan Intertrappean beds of India. The genus Palmophyllum CONWENTZ (1886) was originally proposed for compressions/impressions of palm leaves of uncertain affinities. ACHUTHAN (1967) emended the diagnosis of Palmophyllum to include anatomically-preserved palm laminae. READ & HICKEY (1972) consider Palmophyllum CONWENTZ to be unassignable to palms due to the fragmentary nature of the material.

Palmoxylon SCHENK is an organ genus for anatomically-preserved fossil palm woods. Taxonomically, the genus is in a confused state. As originally circumscribed, Palmoxylon was to include structurally preserved stems with palm-like anatomy and also the roots if found connected to the stems (STENZEL, 1904). However, isolated stems, petioles, and stems with attached petioles and roots have been described as species of Palmoxylon (VAN DER BURGH & MEULENKAMP, 1966; TIDWELL, et al., 1970; 1973). At least one species has been described, Palmoxylon bacillare VAN DER BURGH (1964), that was shown by WEYLAND & KILPPER (1964) not to be a palm at all. Currently, over 160 species of Palmoxylon have been described (e.g, STENZEL, 1904; RAO & ACHUTHAN, 1971; TIDWELL et al., 1971, 1972, 1973). The majority are reported from the Deccan Intertrappean series in India (e.g., RAO & ACHUTHAN, 1971) and numerous Tertiary localities throughout North America, particularly from western and midwestern regions of the U.S.A. (TIDWELL et al. 1971, 1972, 1973).

Few species of Palmoxylon can be related to an extant genus with any degree of reliability. Traditionally, the species have been distinguished based on criteria such as the size, density and form of both the fibrous strands and vascular bundles from different regions in the stem, their fibrovascular ratio, relative proportion of the xylem and phloem sheaths, shape of the fibrous phloem sheath in cross section, presence or absence of fibrous bundles and stegmata, form of parenchyma surrounding the vascular bundles, and number and position of the wide metaxylem vessels. RAO & ACHUTHAN (1971) and TOMLINSON & KLOTZ (1978) have discussed the problems of fossil palm stem systematics and have pointed out that the characters on which species of Palmoxylon are distinguished change both qualitatively and quantitatively within a single stem. A good illustration of this point is found in a paper by WATERHOUSE & QUINN (1978). These authors show four cross sections from different levels and regions of stems of the extant species Archonthophoenix cunninghamiana (Wendl.) Wendl. & Drude. If fragments of these stems were found as permineralizations, undoubtedly at least three Palmoxylon species would be described from this single species.

The abundance of Palmoxylon species and the inclusion of isolated stems, petioles, and stems with attached petioles and roots within the the same genus makes comparison among Palmoxylon species difficult. The result is virtually meaningless with respect to both fossil and extant palm systematics. To compare Uhlia to all species of Palmoxylon would be an astronomical task. Uhlia is, therefore, compared only with fossil palm species, particularly those from Eocene localities in western North America.

Palmoxylon macginitiei and P. edenense described by TIDWELL et al. (1971, 1973) from the Middle Eocene Green River Formation in Wyoming are significant in representing two of the most complete fossil palms to be reported. Like Uhlia, both species consist of a stem (up to four feet long) with attached petiole bases and a basal root zone. The petioles in P. macginitiei are C-shaped in cross section, 10 cm broad X 2.5 cm at its thickess point and have fibrous bundles scattered throughout the ground tissue. Vascular bundles are identical to those of Uhlia in size and overall bundle morphology. Stems of P. macginitiei differ from Uhlia in having larger central vascular bundles, two or sometimes three metaxylem vessels, narrower metaxylem vessels, stegmata absent, and vessels with scalariform perforation plates.

Only the stems of Palmoxylon edenense have been described (TIDWELL et al., 1973). Central vascular bundles are smaller and the metaxylem vessels are narrower than those in Uhlia. Also, vessels have scalariform perforation plates. Fibrous strands occur in the central ground tissue of this species, but stegmata are reportedly absent (TIDWELL, et al., 1973). The habit of both these species has been interpreted to be similar to that of Nypa or Serenoa (TIDWELL, et al., 1973).

Discussion

The diagnosis of Uhlia allenbyensis includes information from stems, petioles, and roots. At least one attached petiole shows a central vascular bundle with a divided phloem strand. The isolated petioles show an intergradation of characters with respect to ground tissue and bundle morphology. Differences in size, ground tissue anatomy, and bundle structure among the specimens may reflect the level of section or age. TOMLINSON (1961) and MENON (1968) have noted that the structure of the leaf axis varies from its insertion to distal levels. Most descriptions of extant petiole anatomy are from sections of mature plants taken from a standard level (i.e., just below the insertion of the laminae or lowest leaflet (TOMLINSON, 1961) or midway between base and insertion of the laminae (KLOTZ, 1978). The more compact ground tissue in the smaller petiole fragments and type "a" petioles possibly reflect the distance from the petiole base to more distal levels and therefore is a developmental phenomenon. WATERHOUSE & QUINN (1978) and RICH (1987) have demonstrated that ground parenchyma cell size in stems decreases with increasing height.

With respect to bundle structure, KLOTZ (1978a) has pointed out the difficulties and uncertainties in determining the number of wide vessels in extant palm petioles. Vessel counts in extant palms are usually taken from central bundles; however, because of the fragmentary nature of the fossil material, it is often impossible to know if the fragments represent a central position. Also the presence of a fibrous partition in bundles of extant palm petioles is usually described from central bundles of mature specimens, whereas in the fossil material the age of the specimen is not known. Remnants of a sclerotic multicellular hair are found on one isolated petiole and the small type "a" petioles. Their absence from attached petioles may be explained by the level of section of the plant organ. In extant palms, hairs are often not uniformly distributed on the leaf (TOMLINSON, 1961).

Anatomical variability with respect to ecology, age of the plant, and level of section of the plant organ in extant palms is not well understood, making the interpretation of fossil remains difficult. Anatomy of only about 10% of living palms was studied by TOMLINSON (1961) and several isolated studies have been done since (UHL, 1972, 1978; TOMLINSON, 1966, 1969; UHL & DRANSFIELD, 1987), but the vast majority of extant palms have yet to be described anatomically.

Further work on extant palms with respect to development, anatomical variation among different aged individuals in a single population, and ecology will provide much needed anatomical information for use in studies of permineralized palms. Previous work on the fossil genus Palmoxylon Schenk and its numerous species (e.g. STENZEL, 1904) illustrates the problems imposed by the uniformity of stem anatomy in this family.

The description of Uhlia allenbyensis is based on attached vegetative and associated organs. Based on comparison to extant palms, Uhlia appears to be most similar to the fan-leaved coryphoid palms, but displays a unique suite of characters that allows its recognition as a new taxon. These characters are consistent with the subfamily Coryphoideae Griffith (sensu UHL & DRANSFIELD, 1987).

According to the most current systematic treatment of palms, the 39 genera comprising the Coryphoideae are subdivided into three tribes that appear to be natural groups: the Phoeniceae Drude, Corypheae, and Borasseae (UHL & DRANSFIELD, 1987). Rhapidophyllum, Brahea, and Serenoa belong to the Corypheae (Table III, 1); however, Rhapidophyllum is placed in the subtribe Thrinacinae Beccari based on the presence of flowers with free carpels and styles. In contrast, flowers of Brahea and Serenoa have free carpels but fused styles which places them in the more advanced subtribe Livistonae Saakov. The fossil appears to share several features with the three genera Rhapidophyllum, Brahea, and Serenoa; however, fossil palm flowers and fruits have not yet been found in the chert. Consequently, unequivocal assignment of the fossil to a subtribe will have to await the discovery of floral parts.

In the present study, the Princeton palm remains have been described and compared within the taxonomic framework of extant palms, rather than simply as organ genera, e.g., Palmoxylon. The vegetative anatomy of the Princeton stems, petioles, roots, midribs, and laminae were directly compared to extant palms using vegetative characters described by TOMLINSON (1961) for modern palms. These remains represent the most well-preserved and anatomically known palm megafossils to be described from a single fossil locality. The present study emphasizes the need for continued detailed monographic studies regarding the vegetative anatomy of extant palm genera. Likewise, future studies of silicified fossil palm stems from a particular locality should, where material is available, fully document anatomy along entire lengths of individual organs in order to better delimit fossil species.

Plate III, 1

Uhlia allenbyensis gen. et sp. nov., stem anatomy.

Fig. 1. Cross section showing attached petiole base (p), peripheral region (a) with numerous horizontally inserted leaf traces (dark lines), narrow zone with small congested vascular bundles (b), central cylinder (c), and root (r), P1351C No. 10, x 1.7.

Fig. 2. Central vascular bundle showing two wide metaxylem vessels (mv), tyloses (t), protoxylem (pr), and single phloem strand (ph) capped by fibers (pf), P1335B Bot No. 5, x 65.

Fig. 3. Cross section of fibrous strand showing narrow, thick-walled fibers and stegmata (arrow), P1397E1 Top No. 2, x 244.

Fig. 4. Central ground tissue showing lacunae (la) and fibrous strands (fs), P1351B B t No. 15, x 85.

Fig. 5. Periphery of stem showing region "a" with diverging leaf traces (lt) and numerous fibrous strands, P1351B Bot No. 15, x 3.2.

Fig. 6. Region "b" showing small congested bundles and few fibrous strands, P1351B Bot No. 15, x 28.

Fig. 7. Periphery of central cylinder showing incipient leaf traces with associated wide metaxylem vessels (mx), phloem fibers (pf), phloem (ph), and protoxylem (pr). Note compact ground tissue with dark contents and fibrous strands, P1351B Bot No. 15, x 33.

Fig. 8. Incipient leaf trace with two diverging axial bundles (arrows), P1335C Bot No. 5, x 40.

Fig. 9. Distal section showing complete separation of leaf trace (lt) from axial bundles (arrows), P1335C Bot No. 5, x 40.

Fig. 10. Cross section showing possible inflorescence or lateral branch trace. Note halo of small satellite bundles (s) surrounding leaf trace (lt), P1397F No. 1, x 30.

Fig. 11. Vessel member showing scalariform intervascular pitting, P1397E1 Top No. 2, x 210.

Fig. 12. Longitudinal section showing septate phloem fibers, P1351B Bot No. 15, x 172.

Fig. 13. Phloem fibers with longitudinal files of druse-like stegmata, P1351B Bot No. 15, x 136.

Fig. 14. Vessel members from stem showing simple perforation plates and tyloses, P1397E1 Top No. 2, x 88.

Fig. 15. Vessel member showing scalariform perforation with three bars, P1351C side 1 No. 1, x 160.

Fig. 16. Vessel member containing numerous tyloses, P1397E1 Top No. 2, x 200.

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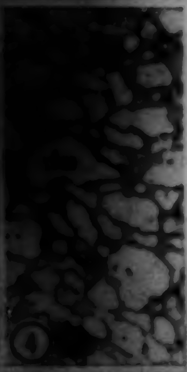

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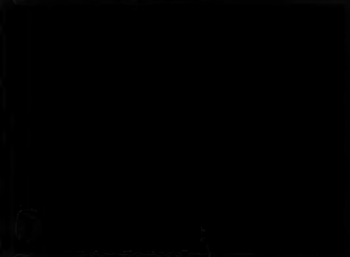

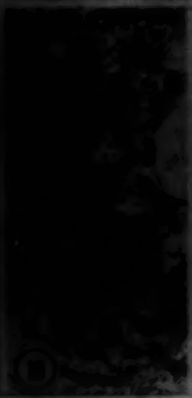

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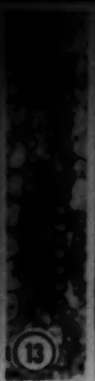

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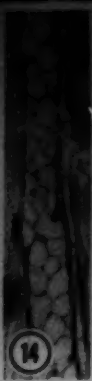

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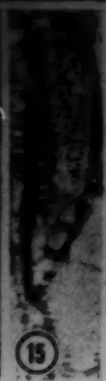

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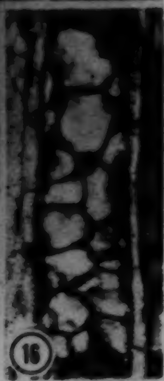

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Plate III, 2

Uhlia allenbyensis gen. et sp. nov., petiole anatomy.

Fig. 1. Oblique cross section showing stem with attached petiole bases (p), P1397E1 Top No. 2, x 1.

Fig. 2. Isolated petiole fragment with evenly-distributed vascular bundles and numerous fibrous strands. Note bundles below the abaxial surface with massive phloem sheaths (arrow), P1274A2 No. 2, x 2.5.

Fig. 3. Petiole possibly split in midregion (arrows), P1390G1 Bot No. 1, x 1.

Fig. 4. Cross section of small triangular isolated petiole with uniformly arranged bundles. Adaxial surface directed toward upper left corner of photo, P1171B1 Bot No. 5, x 3.5.

Fig. 5. Petiole type "a", cross section showing elliptical outline and poorly preserved central region, P1325B Bot No. 0, x 6.

Fig. 6. Vascular bundles from petiole in Figure 4 showing two phloem strands (arrows), one wide metaxylem vessel, poorly preserved ground tissue, and fibrous strands (fs), P1171B Bot No. 9, x 22

Fig. 7. Petiole type "a", vascular bundles from specimen in Figure 5 showing two phloem strands (arrows), one wide central metaxylem vessel (mv) flanked by lateral, narrower vessels and ground tissue with small intercellular spaces, P1325B Bot No. 0, x 59.

Fig. 8. Vascular bundle from petiole in Plate 1, Fig. 1 attached to stem in Figure 1 showing single phloem strand (ph), one wide metaxylem vessel (mv), narrow protoxylem elements (pr), and phloem (pf) and xylem sheaths, P1397E1 Top No. 2, x 70.

Fig. 9. Bundle from petiole in Figure 2 showing one wide metaxylem vessel, undivided phloem strand, aerenchymatous ground tissue and fibrous strands (fs) of variable size, P1274A2, x 56.

Fig. 10. Longitudinal section showing lacunae and chain-like partitions of narrow cells and fibrous strands (arrow), P1387D1 Bot No. 1, x 51.

Fig. 11. Narrow inconspicuous median fibrous partition (arrow) in phloem (ph) of vascular bundle from petiole in Figure 2, P1274A2 No. 2, x 44.

Fig. 12. Longitudinal section showing sieve tube members (sm) with lateral oval to elliptical sieve areas (arrow), P1387D1 Bot No. 1, x 330.

Fig. 13. Longitudinal section of vessel members showing very oblique end walls with sclariform perforations, P1387D1 Bot No. 1, x 330.

Fig. 14. Remnants of hair or peltate scale (?) from petiole in Figure 5 showing base (hb) composed of thick-walled cells, P1325B Bot No. 0, x 275.

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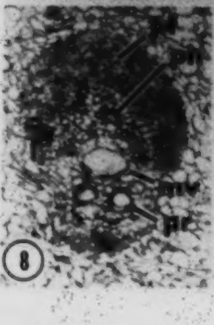
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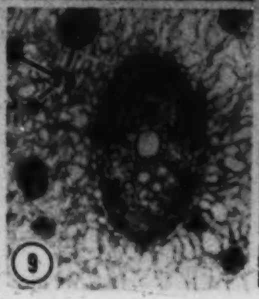
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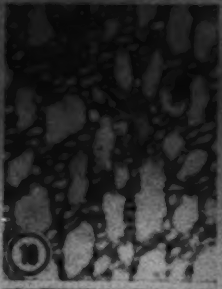
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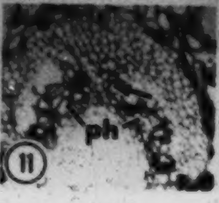
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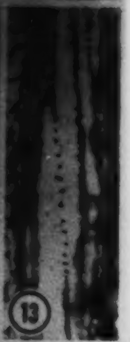
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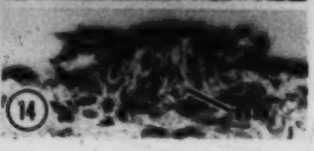
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Plate III, 3

Uhlia allenbyensis gen. et sp. nov., petiole anatomy.

Fig. 1. Abaxial surface of attached petiole showing peripheral series of fiber strands and inner evenly-spaced vascular bundles with massive radially-extended phloem sheaths (ps). Single metaxylem vessel at arrow, P1351C No. 10, x 47.

Fig. 2. Abaxial surface of isolated petiole showing internal structure identical to the attached petiole in Figure 1. Note scattered fiber strands in ground tissue (fs) and single wide metaxylem vessel (arrow), P1274A2 No. 0, x 41.

Fig. 3. Isolated petiole fragment in oblique cross section with preserved aerenchyma on the left and poorly preserved, collapsed ground tissue on right, P1171 SL 5005, x 27.

Fig. 4. Adaxial surface showing fibrous strands in compact tissue, vascular bundle with one wide metaxylem vessel (mv), narrow protoxylem (pr), phloem strand with median sclerotic partition (arrow), fibrous bundle sheath (bs) interrupted at level of metaxylem by parenchyma, and aerenchymatous ground tissue, P1274A2 No. 0, x 41.

Fig. 5. Petiole showing central vascular bundle in lacunose ground tissue (stars) with possible oblique fibrous partition in phloem (arrow), P1274A2 No. 2, x 38.

Fig. 6. Vascular bundle showing median fibrous partition (arrow), P1274A2 No. 0, x 47.

Fig. 7. Central vascular bundle with one wide metaxylem vessel, two phloem strands divided by central partition, remnants of narrow sclerotic elements in phloem (arrows), and fungi in ground tissue, P1197D Bot No. 0, x 43.

Fig. 8. Central vascular bundle from attached petiole in oblique cross section showing median fibrous partition (arrow), P1387D1 Bot No. 2, x 62.

Fig. 9. Attached petiole showing abaxial epidermis (e), fibrous strand (arrow), 4-5 layers of compact, thin-walled subepidermal cells, and radial files of larger thin-walled cells, P1397F No. 1, x 280.

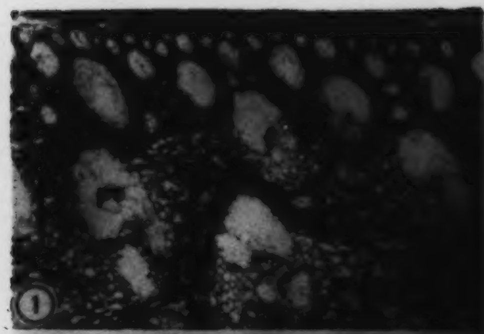
Fig. 10. Isolated petiole showing abaxial thick-walled epidermal (e) and subepidermal cells and fiber strands (fs), P1274A2 No. 0, x 280.

Fig. 11. Attached petiole showing thick-walled abaxial epidermis and subepidermal cells representing similar age as isolated petiole in Figure 10 and older than specimen in Fig. 9, P1351B Bot No. 15, x 280.

Fig. 12. Oblique cross section of adaxial surface of isolated petiole showing thick-walled epidermis (e) and extensive periderm-like layer composed of external thin-walled cells and internal thick-walled cells, P1124D Bot, SL 5528, x 110.

Fig. 13. Periderm-like layer of stem, P1351B Bot No. 15, x 108.

Fig. 14. Fungal hyphae in bundle sheath (bs) and adjacent ground tissue (gt) located in abaxial surface of specimen in Figure 2, P1274A2 No. 0, x 470.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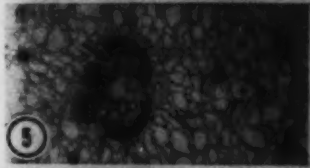
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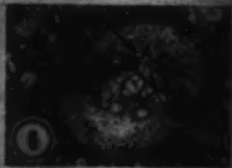
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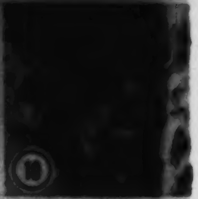
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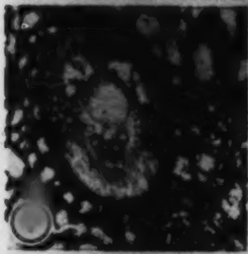
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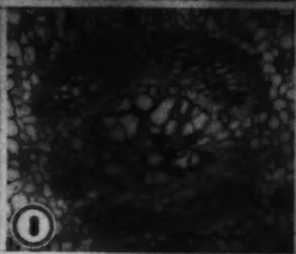
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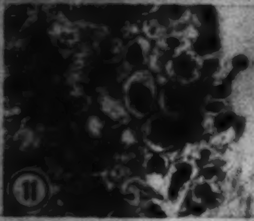
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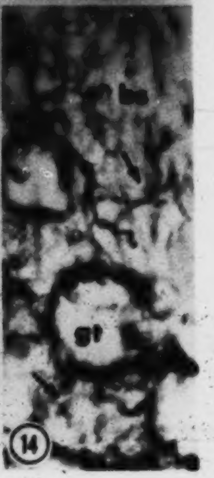
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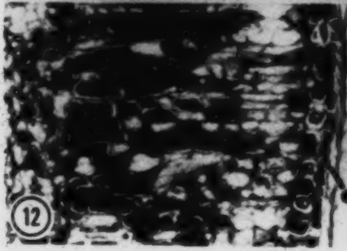
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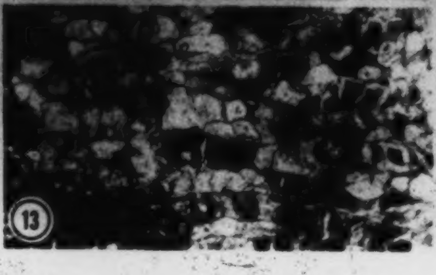
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Plate III, 4

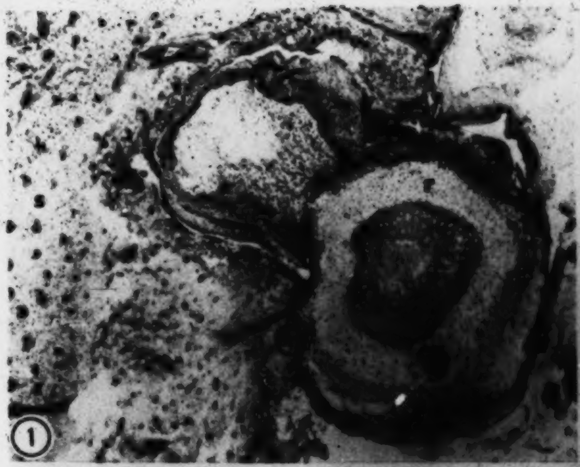
Uhlia allenbyensis gen. et sp. nov., root anatomy.

Fig. 1. Cross section of stem (s) with attached root (r), P1397D1 Top No. 9, x 8.5.

Fig. 2. Cross section of attached root showing medullary vessels (arrows) and scattered cells with dark contents in the inner and middle cortex (mc), P1397D1 Top No. 9, x 35.

Fig. 3. Cross section showing medullated polyarch stele, inner cortex (ic) of radially-aligned cells, radially-extended lacunae (asterisks) in middle cortex (mc), and 3-layered outer cortex (oc), P1124E Bot No. 0, x 35.

Fig. 4. Stele cross section showing radial series of vessels (v) alternating with phloem strands (ph), endodermis (en), and pericycle (pe), P1124G Bot No. 0, x 35.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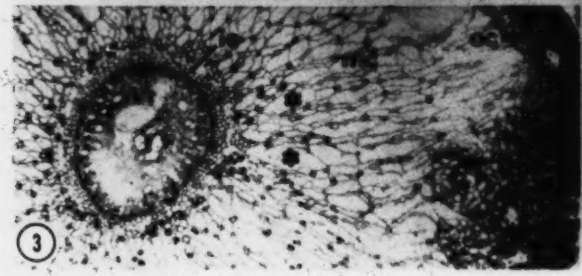
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Plate III, 5

Associated midribs and laminae

Fig. 1. Small abaxial midrib (mr) showing three central vascular bundles and portions of attached laminae (l) infected with fungus. Note empty perithecia (arrows), P1360D Top No. 1, x 28.

Fig. 2. Adaxial midrib with attached laminae showing numerous central vascular bundles (some confluent) and a single band of expansion tissue (et), P1263B Bot No. 5, x 13.

Fig. 3. Midrib bundles showing one wide central metaxylem vessel (mv) flanked laterally by one or more narrower trachery elements, two phloem strands (ph), peripheral fibrous strands, and fungal perithecium (arrow), P1263C No. 6, x 30.

Fig. 4. Abaxial midrib showing three separate central vascular bundles, small hypodermal vascular bundles and fibrous strands, and hairs (arrows), P1171B2 Bot No. 6, x 27.

Fig. 5. Close-up of midrib hair with elliptical base (hb) of thick-walled cells and distal expanse of thin-walled cells (tc), P1277F side 2 No. 6, x 170.

Fig. 6. Cross section of dorsiventral lamina showing thick adaxial cuticle (cu), adaxial palisade (pa), fibrous strands, abaxial stomata (arrows), and centrally-located veins independent from each surface, P1345C Top No. 0, x 115.

Fig. 7. Lamina attached to large midrib in Figure 2 showing bundle structure identical to that of midribs. Note fibrous strands nearly equal in size, shape, and number below each surface, P1263C No. 9, x 60.

Fig. 8. Cross section of lamina showing epidermis (e), single-layered hypodermis (h) below each surface, fibrous strands (fs) adjacent to each hypodermis, and large vein with single wide vessel and sclerotic parenchyma of bundle sheath (arrow), P1345C Top No. 0, x 160.

Fig. 9. Paradermal section of abaxial surface showing diffuse, mostly intercostal distribution of stomata and stegmata associated with fibers of large vein (arrow), P1277F side 2 No. 15, x 110.

Fig. 10. Paradermal section showing stomatal apparatus with guard cells (gc), terminal subsidiary cells (ts), and elongate epidermal cells (e) with straight to slightly sinuous walls, P1789I Top No. 0, x 320.

Fig. 11. Paradermal section showing four L-shaped cells surrounding the substomatal chamber (su), P1277F side 2 No. 9, x 320.

Fig. 12. Cross section showing slightly sunken stomata in abaxial epidermis and epidermal cells, P1345C Top No. 0, x 300.

Fig. 13. Paradermal section showing narrow and wide transverse veins and major vein flanked by 3-4 minor veins, P1277F side 2 No. 15, x 49.

Fig. 14. Sclerotic elements adjacent to longitudinal and transverse veins, P1277F side 2 No. 15, x 300.

Fig. 15. Paradermal section showing fungal perithecia in cross section, P1277F side 2 No. 8, x 49.

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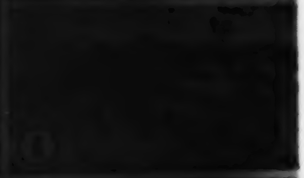

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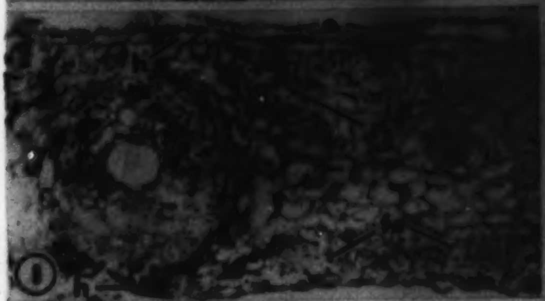
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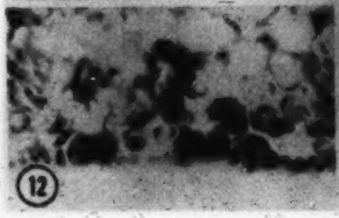
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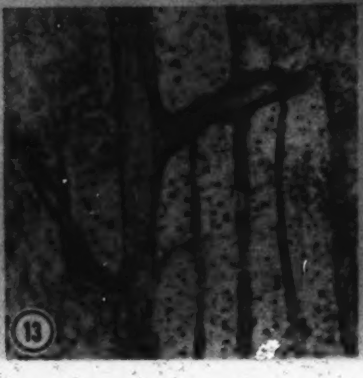
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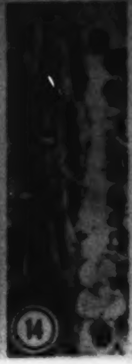
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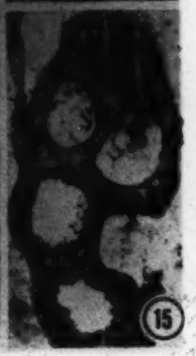
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Plate III, 6

Extant palm anatomy

Fig. 1. Rhapidophyllum hystrix, distal cross section of petiole showing vascular bundles with narrow metaxylem vessels, fibrous bundle sheath, phloem strand divided by median fibrous partition, and superficial hairs (arrows), R.H. No. 1, x 59.

Fig. 2. Serenoa repens, distal cross section of petiole showing vascular bundles with one central wide vessel flanked by one or more narrower tracheary elements, and xylem and phloem sheathed by fibers, S.R. No. 1, x 59.

Fig. 3. R. hystrix, proximal cross section of midrib showing central single large vascular bundle with massive fibrous sheath and narrow tracheary elements surrounded by smaller bundles. Lateral bundles with fused bundle sheaths, R.H. No. 3, x 56.

Fig. 4. S. repens, distal section of midrib showing small size and three central vascular bundles, S.R.(D) No. 1, x 42.

Fig. 5. S. repens, proximal cross section of midrib showing larger size, numerous central vascular bundles (many confluent), one band of expansion tissue, and vascular bundles with one wide central metaxylem vessel flanked by one or more narrow tracheary elements, S.R.(P) No. 1, x 42.

Fig. 6. R. hystrix, paradermal section showing narrow transverse veins and major vein flanked by 4 minor veins, R.H. No. 2, x 49.

Fig. 7. R. hystrix, sclerotic elements adjacent to longitudinal vein, R.H. No. 1, x 300.

Fig. 8 S. repens, narrow transverse veins in lamina and major vein flanked by 3 minor veins, S.R. (2) No. 1, x 49.

Fig. 9. S. repens, sclerotic elements with dark contents next to longitudinal vein, S.R. No. 1, x 300.

Fig. 10. R. hystrix, cross section of dorsiventral lamina showing thick adaxial cuticle, singled-layered hypodermis below each surface, adaxial palisade, abaxial stomata, numerous adaxial anticlinally-extended fibrous strands, centrally located veins, and hair (arrow), R.H. (1) No. 2, x 115.

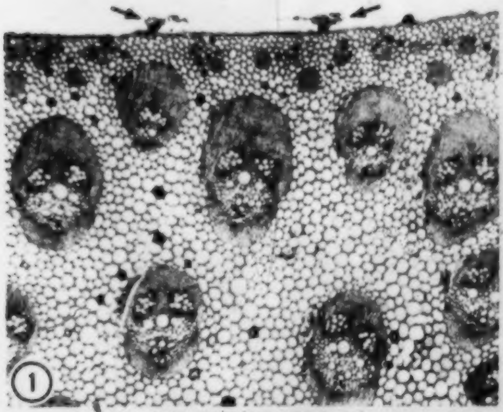
Fig. 11. R. hystrix, paradermal section showing four L-shaped substomatal cells (su), R.H. No. 2, x 320.

Fig. 12. R. hystrix, stomatal apparatus in paradermal section. Note two lateral and two subtriangular-shaped polar subsidiary cells, R.H. No. 2, x 320.

Fig. 13. S. repens, cross section of isolateral lamina showing major vein with one wide metaxylem vessel flanked by narrower tracheary elements, stomata in both surfaces, and cylindrical fibrous strands below each surface, S.R. No. 4, x 115.

Fig. 14. S. repens, paradermal section showing two C-shaped cells (arrow) surrounding substomatal chamber and stomata in different planes of section, S.R. (2) No. 1, x 320.

Fig. 15. S. repens, two hairs showing base of thick-walled cells and distal shield-like expanse of thin-walled cells in shallow depression of petiole abaxial epidermis, S.R. No. 1, x 178.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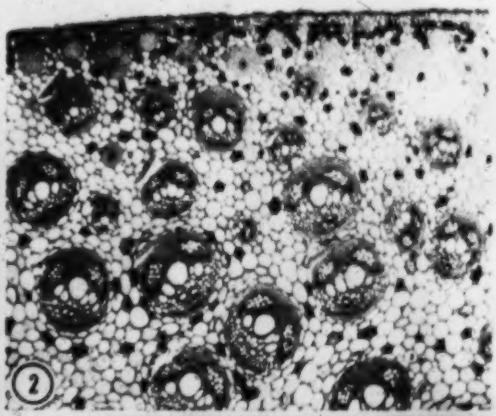
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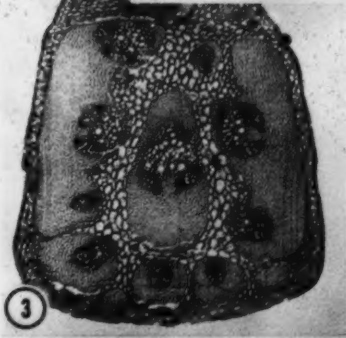
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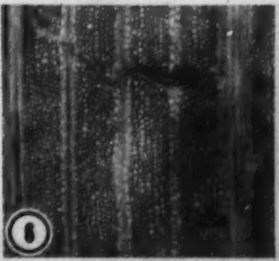
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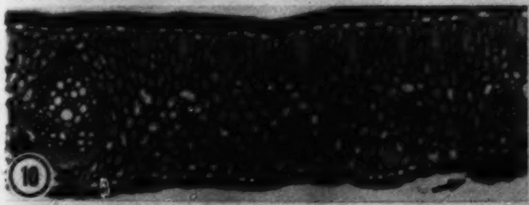
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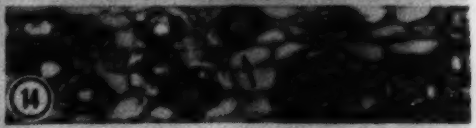
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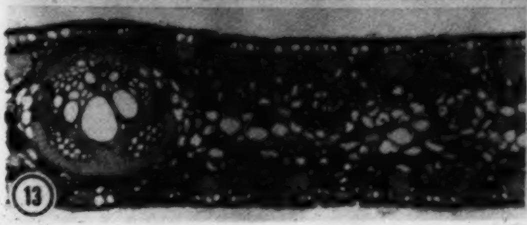
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Table III, 1. Classification of tribe Corypheae. (after Uhl & Dransfield, 1987).

SUBFAMILY: CORYPHOIDEAE Griffith

TRIBE: CORYPHEAE Martius

Subtribe: Thrinacinae Beccari

1. *Trithrinax* (*Diodosperma*)
2. *Chelyocarpus* (*Tessmanniodoxa*, *Tessmanniophoenix*)
3. *Cryosophila* (*Acanthorriza*)
4. *Itaya*
5. *Schippia*
6. *Thrinax* (*Hemithrinax*)
7. *Coccothrinax* (*Haitiella*, *Thrincoma*, *Thringis*)
8. *Zombia* (*Oothrinax*)
9. *Trachycarpus*
10. *Rhapidophyllum*
11. *Chamaerops* (*Chamaeriphe*, *Chamaeriphes*)
12. *Maxburretia* (*Liberbaileya*, *Symphyogyne*
13. *Guihaia*
14. *Rhapis*

Subtribe: Livistoninae Saakov

15. *Livistona* (*Saribus*, *Wissmannia*)
16. *Pholidocarpus*
17. *Johannesteijsmannia* (*Teysmannia*)
18. *Licuala* (*Dammera*, *Pericycla*)
19. *Pritchardiopsis*
20. *Pritchardia* (*Eupritchardia*, *Styloma*)
21. *Colpothrinax*
22. *Acoelorraphe* (*Acanthosabal*, *Paurotis*)
23. *Serenoa* (*Diglossophyllum*)
24. *Brahea* (*Erythea*, *Glaucothea*)
25. *Copernicia* (*Arrudaria*, *Coryphomia*)
26. *Washingtonia* (*Neowashingtonia*)

Subtribe: Coryphinae Beccari

27. *Corypha* (*Codda-Pana*, *Gembanga*, *Taliera*)
28. *Nannorrhops*
29. *Chuniophoenix*
30. *Kerriodoxa*

Subtribe: Sabalinae Martius

31. *Sabal* (*Inodes*)

Table III, 2. Comparison of Uhlia and associated leaf remains to extant non-corypholid palms with central fibrous strands in the stem. Data from Tomlinson (1961); Klotz (1977, 1978a, b); Uhl & Dransfield (1987).

	Stem		Laminae										
											Veins(large)		
Genus	# Phloem strands	#W.M.V.	Leaf Form	Symmetry	Hairs	Hypodermis	Shape & Distrib. Fibrous Strands	Chlorenchyma	Fiber Sclereids	Substomatal Cells	Position	Inner Bundle Sheath	# Phloem Strands
Bactris (189)	1	1 or 2	Pinn.	Dorsi.	Ad. & ab. short, uniseriate stalk; basal cells t.w.	1 layer	Massive cyl.;alt. w/veins at same level	Ad. palisade	Abundant throughout mesophy.; mostly in hypod.	>4	Ab. mesophy.	Cont.	Several irreg.
Cocos (174)	1	2	Pinn.	Dorsi.	3-4 inflated epid. cells sunken in circ. depression; cells	2 layers ad.;1 layer ab.	Fibers non-septate, irreg. . usu. ad., ab.	Ad. 3 layers	--	4 L-shaped	Ab. mesophy.	Cont.	2 lg. ab.; 2 sm. lateral
Leopoldinia (87)	1	1 or 2	Pinn.	Dorsi.	--	1 layer	Fibers solitary in mesophy. or in sm. grps.	Ad. 2 layers	--	4 L-shaped	Ab. mesophy.; independ. of surface	Cont.	2
Phytelephas (199)	1	2 or 6-12	Pinn.	Dorsi.	--	Indistinct	Fibers solitary or in sm. grps. of 3-4	Palisade --	--	4 L-shaped	Ad. mesophy.	Cont.; 1 layer	2

Pinn. = pinnate
Dorsi. = dorsiventral
Ad. = adaxial
ab. = abaxial
t.w = thin-walled

cyl. = cylindrical
strds. = strands
alt. = alternating
mesophy. = mesophyll
hypod. = hypodermis

cont. = continuous
irreg. = irregular
epid. = epidermis
circ. = circular
usu. = usually

sm. = small
lg. = large
grps. = groups
independ. = independent
adj. = adjacent

equidist. = equidistant
arrange. = arrangement
interr. = interrupted
metaxyl. = metaxylem
W.M.V. = wide metaxylem vessels

indist. = indistinct

Numbers in parentheses refer to classification of Uhl & Dransfield (1987)

Table III, 2. Continued. Comparison of Uhlia and associated leaf remains to extant non-coryphoid palms with central fibrous strands in the stem. Stem and laminae. Data from Tomlinson (1961); Klotz (1977, 1978a, b); Uhl & Dransfield (1987).

	Stem		Laminae									Veins(large)	
Genus	# Phloem strands	#W.M.V.	Leaf Form	Sym-metry	Hairs	Hypo-dermis	Shape & Distrib. Fibrous Strands	Chlor-enchyma	Fiber Sclereids	Sub-stomatal Cells	Position	Inner Bundle Sheath	# Phloem Strands
Pinanga (129)	1	1	Pinn.	Dorsi.	Ad. & ab.; base sunken w/4 tiers of sclerotic cells	Absent or indist.	Solitary or in sm. ad. strds.; abundant	Palisade indist.	--	--	Ab. mesophy.; lg. adj. to ab. epid.	Cont.	2-4
Salacca (46)	1	1	Pinn.	Dorsi.	Ab.; base sm., few irreg. sclerotic cells; distal flattened filament of t.w. cells	--	Solitary or in groups of 2-3 adj. to epid.	Ad., indist.	--	--	Equidist. from each surface	?	2
Wallichia (76)	1	2	Pinn.	Dorsi.	Sclerotic cylinder around central t.w. cells	1 layer	Absent from some spp.; freq. in wide bundles alt. w/veins	Ad. palisade	--	No uniform arrange.	Ad. mesophy.	Interr. at level of metaxyl. by sclerotic parenchyma	1
Uhlia (fossil)	1	2	Fan	Dorsi.	-- ?	1 layer	Cyl.; ad. smaller, more numerous than ab.; adj. to hypod.	2-4	--	4 L-shaped	equidist.	Interr. at level of metaxyl. by sclerotic parenchyma	2

Table III, 3. Comparison of *Uhlia* and associated leaf remains to extant non-coryphoid palms with central fibrous strands in the stem. Midrib and petiole. Data from Tomlinson (1961); Klotz (1977, 1978a, b); Uhl & Dransfield (1987).

Genus (#)	Midrib		Petiole				
	Central Vascular Bun[illegible]	Expansion Tissue	Hairs	# W.M.V.	# Phloem Strands	Central Fiber Strands	Bundle Sheath
Bactris (189)	Surrounded by common fibrous cylinder	2 bands opposite rib; add. ad. & ab. bands in lamina	Base of sclerotic, irreg. cells; distal filamentous indumentum of t.w. cells	1	2	+	Phloem fibrous;xylem parenchymatous
Cocos (174)	Surrounded by common fibrous cylinder	2 bands opposite rib	Base of sclerotic, irreg. cells; sunken	1	2	--	Phloem fibrous;xylem parenchymatous
Leopoldinia (87)	?	Frequent; bands below each surface	?	2	2	+	?
Phytelephas (199)	Surrounded by common fibrous cylinder	2 bands opposite rib;add. bands in both surfaces	--	2	2	--	Phloem fibrous;xylem parenchymatous
Pinanga (129)	Surrounded by common fibrous cylinder	2 ab. bands opposite rib; 1 lg. median ad. band	+, like lamina	1	2	--	Phloem fibrous;xylem parenchymatous

W.M.V. = wide metaxylem vessel
add. = additional
ad. = adaxial
ab. = abaxial

irreg. = irregular
t.w. = thin-walled
lg. = large
interr. = interrupted

-- = absent
+ = present
sm. = small

Table III, 3. Continued. Comparison of *Uhlia* and associated leaf remains to extant non-coryphoid palms with central fibrous strands in the stem. Midrib and petiole. Data from Tomlinson (1961); Klotz (1977, 1978a, b); Uhl & Dransfield (1987).

	Midrib		Petiole				
Genus (#)	Central Vascular Bundles	Expansion Tissue	Hairs	# W.M.V.	# Phloem Strands	Central Fiber Strands	Bundle Sheath
Salacca (46)	Surrounded by common fibrous cylinder	Indistinct 2 ab. bands; add. sm. bands in both surfaces	--	1	2	--	Phloem fibrous;xylem parenchymatous
Wallichia (76)	Surrounded by common fibrous cylinder	2 ad. bands opposite ribs; add. enlarged cells in both surfaces	Abundant, base sclerotic w/scurfy indumentum	1-2	1	+	Phloem fibrous;xylem parenchymatous
Uhlia (fossil)	Separate; surrounded by peripheral fibrous strands and sm. vascular bundles	1 band opposite ribs	Base multicellular, sclerotic; distal t.w. cells (?)	1	2(1)	+	Phloem & xylem fibrous; interr. at level of metaxylem by parenchyma

Table III, 4. Lamina characters for Brahea, Rhapidophyllum, and fossil (data from Tomlinson 1961; Klotz 1977, 1978a, b; personal observation).

					Stomata		Hypodermis		
Genus (#)	Leaf Symmetry	Hairs on Lamina	Cuticle	Epidermis	Occurrence & Distribution	Guard Cell Length (um)	No. of Cell Layers	Cell Shape (paradermal section)	Cells Surrounding Substomatal Chamber (p.s.)
Brahea (24)	Dorsi. or iso.	+ or -	Fairly thick	Costal & intercostal cells differ both surfaces	Intercostal, most ab. few ad.; diffuse	15-18	1(-2)	Costal cubical or longitudinally extended; intercostal smaller, less uniform	3-5 irreg. cells
Rhapidophyllum (10)	Dorsi.	+	Ad. thick	Ad. uniform; ab. costal & intercostal differ	Intercostal, ab. only; diffuse	24	1	Ad. more or less cubical; ab. smaller than ad.; intercostal cells irreg.	4 L-shaped cells
Fossil	Dorsi.	-	Ad. thick	Ad.?; ab. costal & intercostal differ	Intercostal, only; diffuse	24-27	1(-2)	?	4 L-shaped cells

Dorsi. = dorsivental
iso. = isolateral
ab. = abaxial
ad. = adaxial
irreg. = irregular
Indist. = indistinct
lg. = large
sm. = small
cyl. = cylinder
hypod. = hypodermis
epid. = epidermis
Equidist. = equidistant
Incompl. = incomplete
Compl. = complete
perpend. = perpendicular
occas. = occasionally
mesophy. = mesophyll
Interr. = interrupted
Adj. = adjacent

Table III, 4. Continued. Lamina characters for *Brahea*, *Rhapidophyllum*, and fossil (data from Tomlinson 1961; Klotz 1977, 1978a, b; personal observation).

		Fibrous Strands			Veins			
Genus (#)	Chlorenchyma	Size	Shape	Attachment	Location Within Leaf	Outer Sheath	Inner Sheath	Transverse
Brahea (24)	Indist. palisade	Ad. lg.; ab. sm.	Ad. & ab. cyl.	Ad. to hypod.; ab. to epid.	Equidist. from both surfaces	Incompl.; cubical cells present	Compl.; fibrous	Few; narrow
Rhapidophyllum (10)	Ad. 2-3 layers ab. cells sm.	Ad. lg.; & perpend. to leaf surface	Ad. narrow	Ad. to hypod. (occas. in mesophy.)	Equidist. or slightly toward ab. surface	Not well-developed but lignified cubical cells occur laterally	Incompl.; interr. laterally by lignified parenchyma	Few; narrow
Fossil	Ad. 2-4 layers	Ad. sm.; ab. lg.	Ad. cyl.; ab. cyl.	Ad. to hypod. (occas. in ad. mesophy.)	Equidist. or slightly toward ab. surface	?	Incompl.; interr. laterally by lignified parenchyma	Few; narrow & wide

Table III, 5. Midrib and petiole characters for *Brahea*, *Rhapidophyllum*, and fossil (data from Tomlinson 1961; Klotz 1977, 1978a; personal observation).

	Midrib	Petiole				
Genus (#)	Bundle Arrangement	Hairs	# W.M.V.	Diameter W.M.V. (um)	Xylem Sheath	Stegmata
Brahea (24)	All bundles isolated	--	1	80-90	Parenchyma	Adj. to lg. veins; rarely adj. to sm. veins & fibrous strds.
Rhapidophyllum (10)	Central bundles few, isolated; sm. peripheral bundles w/fused phloem sheath	+	4-6	30-50	Fibers	Adj. to lg. & sm. veins & fibrous strds.
Fossil	Isolated or central bundles confluent	+	1	60-85	Fibers	Adj. to lg. & sm. veins & fibrous strds.

W.M.V. = wide meataxylem vessel
-- = absent
Adj. = adjacent
lg. = large
sm. = small
strds. = strands

Table III, 6. Comparison of Uhlia and associated leaf remains to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987. Classification after Uhl & Dransfield 1987.

Genus (#)	Laminae											
									Veins (Large)			
	Leaf Form	Symmetry	Hairs	Stomata Distribution	Hypodermal Layers	Fiber Strands	Chlorenchyma	Substomatal Cells	Position	Inner Bundle Sheath	# Phloem Strands	Transverse
Trachycarpus (9)	Palm.	Dorsi.	Base massive, multicellular, sclerotic; distal shield-like expanse of t.w. cells	Infreq. ad; ab. diffuse, intercostal	1	Ad. anticlinally extended, adj. to hypod.;ab. cyl., fewer, adj. to epid.or hypod.	Ad. palisade indist.	4 L-shaped	Equidist.	Cont.	2	Infreq.; wide
Chamaerops (11)	Palm.	Dorsi.	Base massive, elliptical, multicellular, sclerotic; t.w. cells marginal, filamentous	Infreq. ad.; ab. diffuse, intercostal	1	Ad. abundant, lg., anticlinally extended; ab. sm. occas. adj. to epid.	Ad. palisade distinct	No uniform arrang.	Equidist.	Interr. at level of metaxylem by sclerotic parenchyma	2	Freq.; wide
Maxburretia* (12)	Palm.	?	Ab. scales	?	?	?	?	?	?	?	?	?
Guihaia* (13)	Palm.	?	Ab. woolly hairs or dotlike scales	?	?	?	?	?	?	?	?	?
Rhapis (14)	Palm.	Dorsi.	Sm. grp. of sclerotic basal cells w/distal flattened filament of t.w. cells	Infreq. ad.; ab. diffuse, intercostal	1	Solitary fibers numerous;rarely in strds.	Ad. palisade indist.	2, kidney-shaped, long axis parallel to stoma	Ab. mesophy.; independ. of surface	Cont.	2	Infreq.; wide

Palm. = palmate
Dorsi. = dorsiventral
t.w. = thin-walled
Infreq. = infrequent
ad. = adaxial

ab. = abaxial
adj. = adjacent
hypod. = hypodermis
cyl. = cylindrical
epid. = epidermis

equidist. = equidistant
Cont. = continuous
lg. = large
sm. = small
occas. = occasional

arrang. = arrangement
Interr. = interrupted
Freq. = frequent
grp. = group
strds. = strands

mesophy. = mesophyll
independ. = independent
Costapalm. = Costapalmate
perpend. = perpendicular
irreg. = irregular

* Anatomy not studied

Table III, 6. Continued. Comparison of Uhlia and associated leaf remains to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. (Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987). Classification after Uhl & Dransfield 1987.

	Laminae											
									Veins (Large)			
Genus (#)	Leaf Form	Sym-metry	Hairs	Stomata Distribution	Hypo-dermal Layers	Fiber Strands	Chloren-chyma	Substo-matal Cells	Position	Inner Bundle Sheath	# Phloem Strands	Transverse
Livistona (15)	Costa-palm.	Dorsi.	Mostly --;occas. elliptical, multicellular, wart-like	Freq. ab.; rarely = on both surfaces	1-2 ad.; 1 ab.	Numerous,ad. & ab.; occas. in mesophy. at level of sm. veins	Compact, indist. palisade	2,kidney-shaped	Equidist. or in ab. mesophy.; adj. to ad. epid.	Cont.	2	Infreq., wide
Pholidocarpus (16)	?	Dorsi.	--	Abundant ab., intercostal diffuse	1-2	Fibers nonseptate abundant; ad. adj. to epid.; ab. in grps. of 2-4; lg. strds. in palisade	Ad. palisade 3-4 layers	2,kidney-shaped; perpend. to stoma	Equidist. near ad. surface	Interr. at level of metaxylem by sclerotic parenchyma	2	Freq. in ab. mesophy.
Johannesteijs-mannia (17)	Palm.	Dorsi.	--	Ab., intercostal diffuse	1	Ad. & ab.; abundant ad. forming sclerotic layer;ab. sm. [illegible]l. often in mesophy.	Ad. 1-2	2-3 sm. sclerotic cells	Equidist.	Phloem fibrous; xylem, sclerotic parenchyma	2	Freq.; in ad. mesophy.; very wide
Licuala (18)	Palm.; Costa-palm.	Dorsi.	Base sclerotic, elliptical, sunken;distal filament of t.w. cells.	Abundant ab., intercostal	1	Ad. & ab.; ab. adj. to epid.	Indist. palisade	No uniform arrang.	Equidist.	Cont.	2	Infreq.; narrow

Table III, 6. Continued. Comparison of Uhlia to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987. Classification after Uhl & Dransfield 1987.

	Laminae											
									Veins (Large)			
Genus (#)	Leaf Form	Symmetry	Hairs	Stomata Distribution	Hypodermal Layers	Fiber Strands	Chlorenchyma	Substomatal Cells	Position	Inner Bundle Sheath	# Phloem Strands	Transverse
Pritchardiopsis* (19)	Costapalm.	Dorsi.	?	Ad. 2	?	Indist. or --	?	?	?	?	?	
Pritchardia (20)	Costapalm.	Dorsi.	-- or base sclerotic, multicellular; distal shield-like expanse of t.w. cells	Ab., intercostal, diffuse	Ad. 3-4; ab. 1-2	Numerous ad. & ab. lg.;adj. to hypod., occas. in ad. mesophy.	Ad.; palisade; ab. cells sm.	2 C-shaped, long axis parallel to stoma; cells lobed at poles	Equidist. occas. ad.	Ab. fibers only	1, rarely 2	Freq. in ab. mesophy.; wide
Colpothrinax (21)	?	Dorsi.	Base multicellular	?	1-2	Lg. ad. girder-like bundles	?	?	Equidist. largest w/fibrous buttresses; smallest w/ ad. buttresses	?	?	?
Acoelorraphe (22)	Palm.	Dorsi.	--	Infreq. ad.; ab. short, irreg. files, intercostal	1	Sm. strds. or irreg. ad. & ab. clusters;ab. cyl., adj. to epid.	1	2, kidney-shaped, parallel to stoma	Equidist.	Cont.	2	Infreq.; narrow
Serenoa (23)	Palm.	Iso.	--	Ab.,diffuse, intercostal	1	Lg. ad. & ab., anticlinally extended or free in ad. mesophy.	Ad. & ab. palisade	2, C-shaped; parallel to stoma	Equidist.	Interr. at level of metaxylem by sclerotic parenchyma	2	Freq.; ?

Table III, 6. Continued. Comparison of *Uhlia* to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987. Classification after Uhl & Dransfield 1987.

	Laminae								Veins (Large)			
Genus (#)	Leaf Form	Sym-metry	Hairs	Stomata Distribution	Hypo-dermal Layers	Fiber Strands	Chloren-chyma	Substo-matal Cells	Position	Inner Bundle Sheath	# Phloem Strands	Transverse
Brahea (24)	Palm.	Dorsi. & Iso.	--	Infreq. ad.; ab. diffuse, intercostal	1-2	Ad. anticlinally extended;ab. cyl., adj. to epid.; fewer	Indist. palisade	3-5 irreg. cells	Equidist.	Cont.;lg. veins w/ fibrous buttresses	2	Infreq.; narrow
Copernicia (25)	Palm.	Iso.	Wart-like, elliptical, multicellular, w/marginal t.w. cells	Ad. & ab., diffuse intercostal	1	Lg. anticlinally extended or sm. ad. & ab. bundles adj. to hypod. or epid.	--	2 cells parallel to stoma	Equidist. independ. of both surfaces	Interr. at level of metaxylem by sclerotic parenchyma	2	Infreq.; occas. in ab. mesophy.
Washingtonia (26)	Costa-palm.	Dorsi.	--	Ab., intercostal, diffuse	2	Ad. lg. anticlin-ally; ab. sm. cyl.; fewer	Indist. palisade	No uni-form arrang.	Equidist. lg. veins w/fibrous butt-resses	Interr. at level of metaxylem by sclerotic parenchyma	2	Freq.; wide
Corypha (27)	Costa-palm.	Dorsi.	--	Ad. & ab., diffuse, intercostal	Ad. 2, ab. 1	Ad. anticlinally extended; ab. sm. adj. to ab. hypod.	Ad. & ab. palisade-like	2-3, kid-ney-shaped	Numerous, attached to ad. hypod. by fibrous buttresses	Cont.	1	Equidist. or in ab. mesophy. ;wide

Table III, 6. Continued. Comparison of Uhlia and associated leaf remains to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987. Classification after Uhl & Dransfield 1987.

	Laminae									Veins (Large)			
Genus (#)	Leaf Form	Symmetry	Hairs	Stomata Distribution	Hypodermal Layers	Fiber Strands	Chlorenchyma	Substomatal cells	Position	Inner Bundle Sheath	# Phloem Strands	Transverse
Nannorrhops (28)	Costa-palm.	Iso.	--	Ab., diffuse, intercostal	Ad. & ab. 3-4	Ad. & ab.; anticlinally extended, adj. to hypod.	Palisade-like	No uniform arrang.	Attached to ad. & ab. hypod. by fibrous buttresses	Phloem fibrous; xylem sclerotic parenchyma	1	Few, narrow
Chuniophoenix* (29)	Palm.	?	Soft, uneven hairs or ab. indumentum	?	?	?	?	?	?	?	?	?
Kerriodoxa* (30)	Palm.	?	?	?	?	?	?	?	?	?	?	?
Sabal (31)	Costa-palm.	Iso.	--	Ad. & ab. diffuse, intercostal	1	Abundant, anticlinally extended; ad. largest	Ad. & ab.; palisade	4 L-shaped	Ad. mesophy.; attached to hypod. by fibrous buttresses;	Cont.	3	Freq.; wide
Fossil	Fan-leaved	Dorsi.	--	Ab., diffuse intercostal	1	Cyl.; ad. smaller more numerous than ab.	Ad. palisade 2-4 layers	4 L-shaped	Equidist.	Interr. at level of metaxylem by sclerotic parenchyma	2	Freq.; wide &

Table III, 7. Comparison of Uhlia and associated leaf remains to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. Midrib and petiole. Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987. Numbers correspond to classification of Uhl & Dransfield 1987*.

Genus (#)	Midrib	Petiole								
		Hairs	# W.M.V.	Diameter W.M.V. (um)	# Phloem Strands	Hypo-dermal Layers	Peripheral Chlorenchyma	Bundle Sheath	Vascular Bundle Distribution	Armature
(9)	Ab. most prominent; central bundles w/common sclerotic cyl.	Same as lamina	1-4	.06-.08	2	1-2	Conspicuous including fiber strds.	Interr. at level of metaxylem by sclerotic parenchyma	Uniformly scattered;not congested at periphery	Small marginal teeth
(11)	Inconspicuous; 1-3 vascular bundles	Same as laminae	1-4	.07-.09	2	1-2	Distinct layer below hypod.	Interr. at level of metaxylem by sclerotic parenchyma	Scattered; peripheral bundles w/ massive fibrous sheaths-not confluent	Numerous short, or straight spines
(12)	Ab. most prominent	Sometimes *	1	.06-.08	2	?	?	?	?	Unarmed
(13)	?	Caducous wooly	?	?	?	?	?	?	?	Unarmed
(14)	Small, ad. prominent; 1 rarely 2 lg. vascular bundles	Same as laminae	1	.05-.07	2		Narrow, very distinct peripheral fibers, strds. infreq.	Cont.	Central V-shaped arc; peripheral bundles congested	Unarmed

ab. = abaxial
adj. = adjacent
t.w. = thin-walled
Infreq. = infrequent
ad. = adaxial
equidist. = equidistant
Cont. = continuous
hypod. = hypodermis
cyl. = cylindrical
epid. = epidermis
arrang. = arrangement
Interr. = interrupted
lg. = large
sm. = small
occas. = occasional
mesophy. = mesophyll
independ. = independent
Freq. = frequent
grp. = group
strds. = strands
irreg. = irregular

* For generic name see Table III, 1.

Table III, 7. Comparison of Uhlia and associated leaf remains to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. Midrib and petiole. (Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987). Classification after Uhl & Dransfield 1987.

		Petiole								
Genus (#)	Midrib	Hairs	# W.M.V.	Diameter W.M.V. (um)	# Phloem Strands	Hypo-dermal Layers	Peripheral Chlorenchyma	Bundle Sheath	Vascular Bundle Distribution	Armature
(15)	Ab. most prominent; several lg. central vascular bundles	Frequent sm. superficial wart-like	1	.09-.10	2	Inconspicuous, sclerotic in petiole base & leaf sheath	Narrow; incl. lg. fiber strds.	Interr. at level of metaxylem by sclerotic parenchyma	Scattered, not congested at periphery	Marginal spines
(16)	Ad. most prominent proximally	Small multicellular base of sclerotic cells;distal filament of t.w. cells	1	.19-.26	2	1-2; sclerotic	Narrow;lg. fiber strds. numerous, congested	Interr. at level of metaxylem by sclerotic parenchyma	Peripheral bundles congested, but separated by ground tissue	Long spines
(17)	?	--	1	.11-.13	2	?	?	?	?	Small marginal teeth
(18)	Ad. most prominent; central bundle embedded in common fibrous sheath ab. w/1 vascular bundle only	Same as lamina but smaller; uniseriate	1	.05-.08 .11-.12	2	Inconspicuous;small-celled	Narrow fiber strds. at periphery	Cont.	Peripheral bundles not congested;w/ massive fibrous sheath	Marginal spines

Table III, 7. Continued. Comparison of Uhlia and asociated leaf remains to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. Midrib and petiole. Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987. Classification after Uhl & Dransfield 1987.

Genus (#)	Midrib	Petiole								
		Hairs	# Wide Meta-xylem Vessels	Diameter (mm)	# Phloem Strands	Hypo-dermal layers	Peripheral Chlorenchyma	Bundle Sheath	Vascular Bundle Distribution	Armature
(19)	Midribs & ribs prominent	--	?	?	?	?	?	?	?	Unarmed
(20)	Most prominent ab.; several large vascular bundles	Same as laminae	1	.13-.14	2	2-3; cells sm.	Narrow; fiber strds. large in periphery	Phloem fibrous; xylem fibrous or parenchymatous	Uniformly scattered; not congested at periphery	Unarmed
(21)	?	?	1(2)	.14-.17	2	?	?	?	?	?
(22)	Most prominent ad.; lg. vascular bundles fused by common sheath	--	1(3)	.10-.13	2	2 conspicuous & lignified	Conspicuous containing lg. fiber strds.	Cont.	Central bundles uniformly scattered; periphery scarcely congested	Curved marginal spines
(23)	Ab. most prominent; central vascular bundles independ.	Sm.; base sclerotic w/ distal expanse of t.w. cells; in shallow depressions	1	.09-.12	2	1-2; lignified	Conspicuous; containing numerous lg. fiber strds.	Interr. at level of metaxylem by sclerotic	Scattered; not congested at periphery	Small marginal teeth
(24)	Ad. & ab. equally prominent; several lg. independ. vascular bundles	--	1	.08-.09	2	?	?	Phloem fibrous; xylem parenchymatous	Uniformly scattered; congested at periphery, confluent bundle sheaths	Small spines

Table III, 7. Continued. Comparison of Uhlia and associated leaf remains to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. Midrib and petiole. Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987. Classification after Uhl & Dransfield 1987.

Genus (#)	Midrib	Petiole								
		Hairs	# Wide Meta-xylem Vessels	Diameter (mm)	# Phloem Strands	Hypo-dermal layers	Peripheral Chlorenchyma	Bundle Sheath	Vascular Bundle Distribution	Armature
(25)	Ad. & ab.. equally prominent; several lg. central vascular bundles	Wart-like multicellular, sunken	1	.11-.13	2	1-2	Narrow	Interr. at level of metaxylem by parenchyma	Peripheral bundles scattered but not congested	Spines
(26)	Ad. & ab. equally prominent; independ. vascular bundles sometimes slightly confluent	Wart-like multicellular, base sclerotic, superficial indumentum of t.w. cells	1	.10-.12	2	2	Narrow, many peripheral fiber strds.	Phloem fibrous;xylem parenchyma	Uniformly scattered; not congested at periphery	Marginal stout spines
(27)	Ad. & ab. equally prominent	?	1-2	.12-.15	1	Very sclerotic	Narrow	Interr. at level of metaxylem by sclerotic parenchyma	Peripheral bundles congested, each w/ wide fiber sheath	Numerous short, marginal spines
(28)	Ad. & ab. equally prominent; central bundles scattered	Wart-like, multicellular, sclerotic	1-4	.06-.08	1	Several	Narrow	Cont.	Uniformly scattered; not congested at periphery	Unarmed

Table III, 7. Continued. Comparison of Uhlia and associated leaf remains to coryphoid palms with petioles containing mostly one wide metaxylem vessel and one or two phloem strands. Midrib and petiole. Data from Tomlinson 1961; Klotz 1977, 1978a, b; Uhl & Dransfield 1987. Classification after Uhl & Dransfield 1987.

Genus (#)	Midrib	Petiole								
		Hairs	# Wide Metaxylem Vessels	Diameter (mm)	# Phloem Strands	Hypodermal layers	Peripheral Chlorenchyma	Bundle Sheath	Vascular Bundle Distribution	Armature
(29)	Ad. & ab. ribs equally prominent, most prominent ab.	Sparse soft, uneven hairs or scales	?	?	?	?	?	?	?	Unarmed
(30)	Ab. most prominent	Caducous indumentum	?	?	?	?	?	?	?	Unarmed
(31)	Ad. most prominent, central bundles scattered	--	1-2	.15-.17	1	2-3; distinct	?; including freq. fiber strds.	Cont.	Uniformly scattered not congested at periphery; fiber sheath well-developed	Unarmed
Fossil	Ad. & ab. equally prominent	Base sclerotic, multicellular	1	.06-.085	1-2	1-2; lignified	Narrow; containing numerous fibrous strds.; ab. w/ 1-2 series of fibrous strds.	Interr. at level of metaxylem by sclerotic parenchyma	Uniformly scattered; not congested at periphery w/ well-developed fiber sheath	Unarmed

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Chapter 4: Vegetative body of a permineralized monocotyledon from the Middle Eocene Princeton chert of British Columbia.*

Introduction

Reports of fossil plants from early Tertiary strata throughout central and southern British Columbia began in the mid-1800's and have continued to the present day (HEER 1865; G.M. DAWSON 1879, 1890, 1895; PENHALLOW 1908; BERRY 1926; RICE 1947; ARNOLD 1955a & b; ROUSE 1962; HILLS 1965; BONEHAM 1968; ROUSE et al. 1971; MILLER 1973; ROBISON & PERSON 1973; BASINGER 1976a & b, 1981, 1984; BASINGER & ROTHWELL 1977; WILSON 1977a & b, 1980, 1988; MATHEWS & ROUSE 1984; STOCKEY 1983, 1984, 1987; STOCKEY & MANCHESTER 1988; ERWIN & STOCKEY 1989, 1990; CEVALLOS-FERRIZ & STOCKEY 1988a & b, 1989, 1990a-c). Vegetative and reproductive organs of dicotyledons, conifers, and ferns have received the most attention, to the virtual exclusion of monocotyledons. Consequently, our knowledge of monocots inhabiting this region during the Middle Eocene is limited and primarily based on compression floras and pollen.

In this paper, we describe the vegetative body of a small permineralized monocotyledon with attached leaves and roots from the Middle Eocene Princeton chert locality, Allenby Formation, in southern British Columbia. Comparison to living monocotyledons shows that the fossil stems alone share similarities with several monocot families (e.g., Iridaceae, Rapataceae, Restionaceae), but leaf anatomy suggests a closer affinity with the Cyperaceae and Juncaceae.

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*A version of this chapter has been submitted to Courier Forschungsinstitut Senckenberg. 1990.

Materials and Methods

Approximately 50 small monocotyledonous stems with attached roots and leaves have been found in chert blocks from the Princeton chert locality. The Princeton locality is in the Allenby Formation, Princeton Group (BONEHAM 1968). This locality is characterized by a 10 m thick section consisting of 49 layers of interbedded chert and coal with an occasional thin ash bed (STOCKEY 1984) that outcrops on the east bank of the Similkameen River, 8.4 km south of Princeton, British Columbia. The site has been referred to as locality "I" (BONEHAM 1968) and the "Princeton chert" (BASINGER & ROTHWELL 1977; STOCKEY 1984). A Middle Eocene age has been reported for the Allenby Formation based on K-Ar dates from volcanic rocks within the Allenby Formation (ROUSE & MATHEWS 1961; MATHEWS 1964; HILLS & BAADSGAARD 1967), palynological correlations (ROUSE et al. 1971; MATHEWS & ROUSE 1984), and studies of fossil insects and freshwater fishes (WILSON 1977a & b, 1978, 1982, 1988).

Specimens are preserved as siliceous permineralizations and were studied using the cellulose acetate peel technique (JOY et al. 1956) modified by use with hydrofluoric acid (BASINGER & ROTHWELL 1977; BASINGER 1981). Peel sections were mounted on microscope slides with Eukitt or Coverbond xylene soluble mounting medium for microscopic examination.

All slides are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Results

Systematic section

Class: Liliopsida

Subclass: Commelinidae

Family: *Incertae sedis*

Genus: *Ethela* gen. nov. Erwin et Stockey

Species: *Ethela sargantiana* sp. nov. Erwin et Stockey

DIAGNOSIS: Short rhizomes, 0.4-1.5 cm in diameter; occasionally with lateral branch traces or small branches, 2.5-3.0 mm wide. Branches histologically similar to main stems. Pith solid, parenchymatous, cell wall thickness variable; including tannin sacs. Central cylinder atactostelic; bundles arranged in three or more irregular cycles. Primary thickening meristem present, not extending to stem center. Bundles primary; collateral, mostly amphivasal; circular to oval-shaped in cross section, 0.06-0.43 mm radially and 0.05-0.27 mm tangentially. Bundle sheath 1-4 cells wide; sheath cells thick-walled parenchyma. Metaxylem in collateral bundles wedge-shaped, several cells wide; in amphivasal bundles, 1 to several cells wide; tracheary elements thin-walled, imperforate(?), 6.0-18.2 um wide; intervascular pitting scalariform. Phloem strand single, located between arms of metaxylem in collateral bundles; including narrow thick-walled cells with dark contents. Thin-walled cells containing dark material (tannin?) scattered in vascular tissues. Leaves with sheathing base, crescentiform, dorsiventral, 0.21- 1.18 mm thick, parallel-veined. Bulliform cells absent. Adaxial epidermal cells rectangular, widest tangentially; abaxial cells 1.5 to 2 times higher than broad, walls straight or wavy(?). Cells of both surface nearly equal in size. Mesophyll mostly spongy parenchyma, including tannin sacs, some appearing thick-walled. Hypodermal fiber strands present along abaxial surface only, attached to epidermis; primary strands 4- to 5-sided, from 4 to 6 cells wide, largest baculiform, narrowest point adjacent to epidermis; secondary strands 2 to 3 cells wide, baculiform. Veins collateral, circular to oval-shaped; major bundles 0.13-0.20 mm radially X 0.10-0.18 mm tangentially alternating with minor bundles 0.08-0.14 mm radially X 0.08-0.09 mm tangentially; arranged in a single row, equidistant from both surfaces in proximal sections, distally smaller veins closer to the abaxial epidermis. Outer bundle sheath parenchymatous, lateral, discontinuous, mostly inconspicuous. Inner bundle sheath fibrous, 1-4 cells wide; mostly one cell wide on flanks of large veins, cells narrow, uniform in size proximally cell walls of variable thickness; cell layers often more numerous at xylem pole; distally cells in outermost layer of xylem sheath wider than inner cells. Inner bundle sheath free or attached to an abaxial fiber strand forming an elongate, bulbiform, girder-like extension with lateral sides concave. Tracheary elements in leaf narrow, poorly preserved, larger elements vessels with long, very oblique scalariform perforation plates. Phloem strand including thick-walled cells with dark contents. Roots 0.5-0.8 mm wide; steles 0.13-0.28 mm wide, medullated, polyarch. Pith fibrous. Vessels angular, vessel members 9-15 um wide X 97-106 um long; intervascular pitting scalariform, reticulate; perforation plates short, oblique, scalariform. Vessels with dark contents.

Holotype: P1382 A1 (Fig. 1).

Paratypes: P1130 A, Bbot, Ctop; Dbot; P1133 Bbot, Ctop; P1182 A, Btop; P1278 Dbot, Etop; P1328 F1bot, G2bot, G3top, H1top; P1382 C1top; P2561 Dtop, Etop; P5421 A, Ebot, Ftop.

Etymology: Genus and species named in honor of Dr. Ethel Sargant for her contributions to our knowledge of monocotyledons.

General Features

Ethela is one of the most abundant and complete permineralized plants recovered thus far from the Princeton chert locality. Specimens are found scattered in the matrix with most slab surfaces showing several different stems in cross section (Pl. IV, 1 Fig. 1, Pl. IV, 3 Fig. 1). Stems are up to 1.5 cm wide, a few show both remnants of attached leaves and roots (Pl. IV, 1 Fig. 1, Pl. IV, 3 Fig. 1), or traces of these organs in the cortex (Pl. IV, 2 Fig. 3), while still others display small lateral branches (Pl. IV, 1 Figs. 2, 5).

In cross section, Ethela is characterized by a solid pith surrounded by a central cylinder containing numerous scattered vascular bundles embedded in parenchymatous ground tissue that includes scattered tannin sacs and intercellular spaces filled with dark contents (Pl. IV, 1 Figs. 1, 3, 4). Aside from a few collateral bundles near the pith, most vascular bundles are amphivasal and each is enclosed by a sclerotic bundle sheath (Pl. IV, 1 Figs. 3, 8, 9).

A relatively wide cortex (Pl. IV, 1 Fig. 3; Pl. IV, 2 Fig. 3) showing two distinct zones is delimited from the central cylinder by an endodermoid layer one to three cells wide (Pl. IV, 1 Figs. 3, 6; Pl. IV, 2 Figs. 3, 8). Adventitious roots diverge from all sides of the stems and show typical monocotyledonous structure in cross (Pl. IV, 2 Figs. 2, 5) and longitudinal section (Pl. IV, 2 Fig. 4). In some specimens the roots have punctured their way through the surrounding leaves (Pl. IV, 1 Fig. 1, Pl. IV, 2 Fig. 1).

Stem Morphology (Pl. IV, Figs. 9-13

Monocotyledons show a wide range of growth forms (HOLTTUM 1955). Some display short rosette stems with crowded leaves and congested internodes, others are rhizomatous, while still others, like many plants in the subclass Arecidae are arborescent. Most descriptive terms, such as bulbs, corms, tubers, and rhizomes, are based on external form. These stems often intergrade, complicating their classification as one type or another (ARBER 1925) and anatomically they are quite similar (e.g., see RUDALL 1984, 1989).

Based on stem morphology and leaf anatomy, Ethela could be interpreted as a bulb or short rhizome. Bulbs are shortened vertical underground stems with several cycles of ensheathing fleshy leaves (RADFORD 1986; RUDALL 1989). As seen in Pl. IV, 1, Fig. 1, Pl. IV, 3, Fig. 1, the fossil stems are surrounded by several overlapping, tightly arranged fleshy leaves with spongy parenchyma. Many bulbs produce at the base one or more inflorescence axes or lateral shoots with narrow scale-like leaves that will develop into bulbs once the parent bulb degenerates (ARBER 1925; RUDALL 1989). Although the vegetative or reproductive nature of the lateral branches in Ethela is not yet known, the plants nonetheless are consistent with this morphology (Pl. IV, 1 Fig. 2).

In a recent study of bulbous Iridaceae, RUDALL (1989) illustrates sections of bulbs that are structurally very similar to Ethela but lack a pith. Bulbs have no pith (ESAU 1965), but the universality of this character is not known. For example, there are some rhizomes with no pith that look like bulbs in cross section (RUDALL 1984). Based on the presence of a pith in Ethela we interpret the fossil stems as short rhizomes with congested internodes and numerous ensheathing leaves.

Stem anatomy (Pl. IV, 1 Figs. 1-14; Pl. IV, 2 Figs. 3, 8)

In cross section, the central cylinder consists of numerous, circular to oval-shaped bundles that are largest near the pith and become smaller and more congested toward the periphery of the central cylinder (Pl. IV, 1 Figs. 1, 3). Surrounding each bundle is a sheath composed of 1-4 layers of thick-walled parenchyma cells polygonal to oval-shaped in cross section (Pl. IV, 1 Figs. 3, 8, 9). Occasionally cells of the outermost layer are larger than those of the inner layers and sheath cells are generally equal to or smaller than cells of the adjacent ground tissue (Pl. IV, 1 Figs. 8, 9). The bundle sheath is sometimes widest opposite the xylem pole (Pl. IV, 1 Fig. 9).

Vascular bundles are all primary in origin. Most bundles are amphivasal; however, some bundles in the inner region of the central cylinder appear to be collateral and probably represent incipient leaf traces (Pl. IV, 1 Fig. 8, arrow). Collateral bundles in cross section show a solid V-shaped xylem strand and a single phloem strand located between the xylem arms (Pl. IV, 1 Figs. 8, 9), whereas in amphivasal bundles the xylem completely surrounds the phloem (Pl. IV, 1 Fig. 8; arrowhead). Tracheary elements are 6.0-18.2 um in diameter, thin-walled, and mostly inconspicuous and not well preserved (Pl. IV, 1 Figs. 8, 9, 11). These elements in longitudinal section have scalariform pitting on the lateral walls (Pl. IV, 1 Fig. 10), but perforations have not been observed. The phloem consists of a group of very narrow cells that in cross section are similar in size making it difficult to distinguish between sieve tubes, companion cells, and phloem parenchyma (Pl. IV, 1 Fig. 10). Associated with the vascular tissues are axially elongated thin-walled cells of variable diameter that are filled with dark contents (Pl. IV, 1 Fig. 11).

Ground tissue in the central cylinder is composed of lignified parenchyma cells with intercellular spaces. Scattered in the ground tissue are cells of variable diameter that are filled with dark contents (Pl. IV, 1 Fig. 13). These cells are identical to those described by ESAU (1977) as tannin sacs or referred to as tannin cells by some authors (e.g., CUTLER 1969).

The cortex is differentiated into outer and inner cortical zones (Pl. IV, 1 Fig. 3; Pl. IV, 2 Fig. 3). The outer cortex is composed of 5-10 layers of very compact, thick-walled cells, polygonal in cross section (Pl. IV, 1 Figs. 3, 7; Pl. IV, 2 Fig. 3), and axially elongated in longitudinal section. The inner cortex is 5-6 times wider than the outer cortex and consists of loosely-packed, thin-walled parenchyma

(Pl. IV, 1 Figs. 3, 4, 14; Pl. IV, 2 Fig. 3). Within the inner cortex are leaf and root traces, plus large circular to oval-shaped cells with dark contents (Pl. IV, 1 Fig. 4) that probably represent tannin sacs similar to those in the central ground tissue (Pl. IV, 1 Fig. 4). Tannin sacs occur less frequently in the outer cortex. Inner cortical cells are generally smaller than those of the outer cortex and in cross section are circular, weakly lobed, or have short, arm- or peg-like extensions (Pl. IV, 1 Fig. 14). In some stems, numerous files of radially aligned cells indicative of a primary thickening meristem occur in the inner cortex adjacent to the endodermoid layer (Pl. IV, 1 Fig. 3, arrows, 6; Pl. IV, 2 Fig. 3), as well as, continuing into the central cylinder (Pl. IV, 1 Fig. 3, arrowhead).

The cortex is delimited from the central cylinder by an endodermoid layer, one to three cells wide (Pl. IV, 1 Fig. 6; Pl. IV, 2 Fig. 3, 8). Endodermoid cells in cross section are thick-walled, square to rectangular or sometimes irregular in shape. Usually all cell walls are evenly thickened, but occasionally only the radial and inner tangential walls are lignified (Pl. IV, 2 Fig. 8). At levels of root divergence, this layer is continuous with the root endodermis (Pl. IV, 2 Fig. 3); however, it is less conspicuous or absent in stem sections at levels through developing leaf bases and lateral branches. Surrounding the stems is a single-layered epidermis composed of radially-elongated, four- to five-sided cells, that occasionally contain dark contents (Pl. IV, 1 Fig. 7). The pentagonal cells show inner walls in the shape of a "v" while the radial walls are mostly parallel to each other (Pl. IV, 1 Fig. 7).

Root anatomy (Pl. IV, 2 Figs. 1-9)

Roots in cross section are polyarch, 0.50-0.80 mm wide, and show a small medullated stele 0.13-0.28 mm wide (Pl. IV, 2 Figs. 1, 2, 5). In the larger roots wide angular metaxylem elements, 9-15 um wide, are arranged in an irregular ring surrounding the pith (Pl. IV, 2 Fig. 5). These cells often have dark contents (Pl. IV, 2 Figs. 1, 2, 5). In longitudinal section, vessel members are relatively short, intervascular pitting is scalariform to reticulate (Pl. IV, 2 Figs. 6, 7), and they have short, oblique, scalariform perforation plates (Pl. IV, 2 Figs. 6, 7).

The phloem is virtually indistinguishable, but probably occurs in small strands that alternate with the protoxylem poles. Associated with the vascular tissues are narrow thin-walled cells with dark contents similar to those found in the vascular bundles of the stems.

The endodermis in cross section consists of a single layer of small, square to rectangular cells, 6-9 X 2 um wide, that show walls either uniformly thickened or with only thick radial and inner tangential walls, the latter cells appearing U-shaped in cross section (Pl. IV, 2 Fig. 5). Neither passage cells in the endodermis nor a distinct pericycle have been observed.

The cortex is solid and composed of radial files of rounded, square to rectangular, thin-walled cells that increase in diameter toward the periphery (Pl. IV, 2 Fig. 1). In most roots, however, the cortex is not preserved and represented by a large space (Pl. IV, 1 Fig. 1; Pl. IV, 2 Figs. 1, 2) or has remnants of broken down cortical cells giving it an aerenchymatous appearance (Pl. IV, 2 Fig. 2). External to the cortex is a hypodermis composed of two to three layers of thick-walled cells (Pl. IV, 2 Figs. 2, 9) that is surrounded by a one-layered epidermis. Epidermal cells are four- to five-sided and slightly larger than the hypodermal cells, but similar in shape (Pl. IV, 2 Figs. 2, 9). The pith of most specimens is fibrous (Pl. IV, 2 Fig. 5).

Several specimens have been found that appear to represent branched roots (Pl. IV, 2 Fig. 1); however, these specimens may represent one root growing through the cortex of another root (i.e. intracortical roots). Intracortical roots have been reported in the Cyperaceae (METCALFE 1971).

Leaf anatomy (Pl. IV, 3 Figs. 1-10)

Leaf remnants attached to the stems are broad, crescentiform, dorsiventral, show parallel venation, and a single-layered epidermis on both surfaces. The most complete specimen shows up to 8 different leaves (Pl. IV, 3 Fig. 1). Because of the limited extent of this specimen, it has not been possible to trace an entire leaf distally to determine its overall morphology. In cross section, adaxial epidermal cells are fairly uniform, cubical to rectangular-shaped and tangentially elongated (Pl. IV, 3 Figs. 2, 6). Abaxial epidermal cells are larger and less uniformly shaped. Cells in the abaxial epidermis located between the vascular bundles and fiber strands are radially-elongated and four- to five-sided (Pl. IV, 3 Figs. 3, 5). The radial walls are either straight or wavy (Pl. IV, 3 Fig. 5); however, the wavy appearance could have resulted from compression of the epidermis. Cells above vascular bundles and fiber strands are smaller and tangentially flattened (Pl. IV, 3 Figs. 3, 5). Glands, trichomes, raphides, or silica bodies have not been observed; however, what appears to be a stomatal apparatus occurs in the adaxial epidermis of one leaf (Pl. IV, 3, Fig. 2, arrowhead). Epidermal cells are occasionally filled with dark contents (Pl. IV, 3 Fig. 8).

In most specimens, distinct hypodermal layers are absent, however in some leaf sections, cells below the adaxial epidermis resemble those of the epidermis (Pl. IV, 3 Fig. 6). Cells of both of these layers appear to have thicker walls than cells of the mesophyll.

Evenly-spaced fibrous strands occur just below the abaxial epidermis (Pl. IV, 3 Figs. 3, 4, 7) and each strand consists of a group of elongate, thick-walled fibers with narrow, oblique, slit-like pits on the lateral walls. Fibrous strands vary in size and shape depending on the level of section. Typically, the largest strands lie opposite the major veins (Pl. IV, 3 Fig. 3). Fiber strand shape in cross section includes circular to oval-shaped strands, subtriangular forms, or narrow, short to long radially elongate strands, or even longer and wider girder-like extensions that connect with the bundle sheath (Pl. IV, 3 Figs. 2-5, 7-9). Following METCALFE'S (1971) terminology for sclerenchyma shapes in leaves of Cyperaceae, the sclerenchyma associated with the veins in distal sections of Ethela most closely resembles abaxial, bulbiform girders with an adaxial cap flanking the xylem (Pl. IV, 3 Figs. 3, 4, 7, 8). However, the fossil girders are narrower and more radially elongated than the bulbiform type illustrated.

The mesophyll is not differentiated into palisade and spongy layers; however, in basal sections this tissue resembles the zonation of the cortex. At this level, the mesophyll consists of compact, thin-walled, parenchyma with small intercellular spaces. However, in more distal sections intercellular spaces are larger giving the entire mesophyll a spongy appearance (Pl. IV, 3 Fig. 9). Scattered throughout the mesophyll are tannin sacs with dark contents (Pl. IV, 3 Figs. 2, 3, 8) resembling those in the stem. In addition, dark contents fill many of the intercellular spaces.

Veins are collateral and are mostly circular to oval-shaped in cross section. Generally two types occur: major bundles, 0.13-0.20 X 0.10-0.18 mm wide, that alternate with minor bundles, 0.08-0.14 X 0.08-0.09 mm wide (Pl. IV, 3 Figs. 3, 4, 7). In basal sections, veins are arranged in a single row equidistant from each surface (Pl. IV, 3 Fig. 3) and each is surrounded by a complete sheath composed of 1-4 layers of narrow thick-walled cells (Pl. IV, 3 Figs. 2, 3). Xylem is composed of a wedge-shaped group of poorly preserved, narrow tracheary elements of nearly uniform size (Pl. IV, 3 Fig. 2). At more distal levels, veins are located nearer the abaxial surface. In most veins, the xylem consists of a small group of inconspicuous angular thin-walled cells (Pl. IV, 3 Figs. 4, 7, 8); however, the large vein in Figure 8 shows two narrow, laterally-placed tracheary elements (arrows), plus several smaller tracheary cells. In longitudinal section, the tracheary elements show scalariform thickenings. From section view it is difficult to tell if these cells are tracheids with scalariform lateral wall pitting or narrow vessels with long very oblique scalariform perforation plates (Pl. IV, 3 Fig. 10), the latter interpretation is accepted here. The phloem usually appears as a dark strand composed of very narrow cells (Pl. IV, 3 Fig. 2). In many veins, cells of the phloem are thick-walled with dark contents (Pl. IV, 3 Fig. 8).

The leaves show a distinct pattern of vascular bundle and fiber strand distribution. Fibrous strands associated with each vein in the most proximal sections are distinct from the veins (Pl. IV, 3 Figs. 2, 3), but more distally these strands unite with the bundle sheath to form girder-like extensions that connect with the abaxial epidermis (Pl. IV, 3 Figs. 4, 7, 8). Located between each girder is a single fibrous strand (primary strand) that is not associated with a vein (Pl. IV, 3 Figs. 3, 4, 7). In addition to the primary strands, smaller secondary strands occur in some specimens (Pl. IV, 3 Fig. 7, arrows).

Comparison to extant taxa

In monocotyledons, leaves and culms exhibit some of the most important diagnostic vegetative characters, whereas stems and roots are structurally more conservative and therefore provide fewer characters of taxonomic value (METCALFE 1960, 1971; TOMLINSON 1961). BROWN (1958) and later METCALFE (1960) established the use of leaf anatomy for the taxonomy of grasses. Leaf anatomy has since been found to be significant in other monocot families (e.g., TOMLINSON 1961, 1969, 1982; AYENSU 1969, 1974; CUTLER 1969; METCALFE 1971; DENTON 1983;

TOMLINSON & WILDER 1984; RUDALL 1983, 1986; RUDALL & BURNS 1989).

Stems and roots of Ethela show morphological and anatomical features consistent with the Liliales, Juncales, and Cyperales, but leaf anatomy is most similar to the Juncales and Cyperales. Characters of importance relate to leaf symmetry, size, and shape in cross section; presence or absence of silica bodies and their shape and distribution; morphology of epidermal cells, bulliform cells, and hairs; mesophyll differentiation; vascular bundle morphology and distribution; bundle sheath structure; sclerenchyma form and distribution; plus vessel distribution and degree of end wall specialization.

Juncales

In surveying the vegetative anatomy of Juncales, CUTLER (1969) used the classification of HUTCHINSON (1973) thus providing descriptions for Centrolepidaceae, Restionaceae, and Anarthriaceae. Among these families, leaves of Anarthriaceae resemble Ethela in having abaxial girders and adaxial caps flanking the xylem, but differ in lack of abaxial subepidermal strands (CUTLER 1969). Anarthriaceae also differ from Ethela in having abaxial chlorenchyma composed of several layers of elongated "peg-cells" oriented either axially and in long chains or in one layer oriented radially (CUTLER 1969). Tannin is infrequent and probably pathological in origin (CUTLER 1969), whereas tannin sacs are abundant in Ethela.

Thurniaceae differ from Ethela in having small, confluent, inverted bundles associated with the larger veins of the leaf (CUTLER 1969). The xylem poles of these bundles are directed toward each surface rather than directly facing one another as in the inverted bundles of *Iris* and other monocotyledons with ensiform leaves (ARBER 1925; CUTLER 1969).

Leaves of Juncaceae also resemble those of *Ethela*. Like *Ethela*, abaxial epidermal cells in cross section, are 1.5 to two times wider radially than they are broad, but differ from *Ethela* in having only straight anticlinal walls (CUTLER 1969). The anticlinal walls in *Ethela* appear to be both straight and wavy (Pl. IV, 3 Fig. 5), but the wavy appearance of these walls may have resulted from compression of the epidermis prior to or during fossilization. Most large veins in Juncaceae display one to four lateral metaxylem vessels. These cells are conspicuously wider than adjacent vascular cells and show oblique, simple, scalariform, or scalariform-reticulate perforations (CUTLER 1969). Most veins in *Ethela* contain narrow tracheary elements that are similar in size, inconspicuous, and often are not well preserved. In one specimen, however, there is a narrow vessel on each side of the largest vein. Veins with narrow lateral vessels occur in some species of *Juncus* L. (e.g., *J. biglumis* L.) and *Distichia* Nees & Meyen (CUTLER 1969). However, these taxa differ from *Ethela* in having sclerenchyma confined to the bundle sheaths. Presence of tannin and the absence of silica bodies are characters also shared by both *Ethela* and Juncaceae.

Although rare, small sclereids and secretory cells occur in the phloem of certain species of Juncaceae. Thick-walled, pitted cells that probably represent sclerified phloem cells occur in *Ethela*, but secretory cells like those described in Juncaceae have not been recognized. There are thin-walled cells with dark contents associated with the phloem, but the exact nature of these cells is not known.

The most conspicuous character in leaves of Ethela are the abaxial sclerenchyma girders and alternating subepidermal strands. Within Juncaceae, presence of abaxial sclerenchyma girders in the leaves is considered a diagnostic feature in three of the subgenera of Juncus the "Junci genuini", "Junci thalassi", and "Junci poiophylli" of Buchenau (1890) and the genus Oxychloe (CUTLER 1969). These species of Juncus differ from Ethela in having palisade-like chlorenchyma composed of cells 2-4 (-6) times higher than wide arranged in 1-4 or 5 (-7) layers, and the inner bundle sheath restricted to bundle caps in smaller veins, whereas in larger veins the sheath is complete and widest opposite the phloem (CUTLER 1969). Oxychloe differs from Ethela in having parallel-sided girders, 2-5 cells wide, that are widest next to the epidermis, oval to circular-shaped leaves, two to four angular vessels on the flanks of the large veins, and lacks tannin sacs (CUTLER 1969). In addition, both Juncus and Oxychloe apparently lack individual strands that are associated with a vascular bundle (CUTLER 1969) as in Ethela.

Cyperales

Abaxial sclerenchyma girders and strands occur in leaves of Graminae (METCALFE 1960). Ethela differs from species of Graminae in having veins with a U-shaped abaxial fibrous xylem cap that is independent of the adaxial epidermis, a sclerenchyma type that apparently does not occur in grasses (METCALFE 1960; RENVOIZE 1982a, b, c 1983, 1985a-c, 1986a, b, 1987a, b). Grass rhizomes show vascular bundles with two to three wide lateral metaxylem vessels (METCALFE 1960). Vessels in Graminae are in all plant organs and have mostly simple perforation plates (CHEADLE 1955; WAGNER 1977; DAHLGREN & CLIFFORD 1982). Tracheary elements in Ethela are narrow, nearly uniform in size, and as interpreted here, have scalariform perforations in the roots and leaves.

Sclerenchyma shape and distribution in Ethela most closely resembles genera in Cyperaceae e.g., Neesenbeckia Levyns & Machaerina Vahl. (METCALFE 1971). However, unlike most Cyperaceae, veins in Ethela lack lateral metaxylem vessels that are conspicuously wider than neighboring cells (METCALFE 1971). Most cyperaceous genera have silica bodies in the epidermal cells above the sclerenchyma (METCALFE 1971). Silica bodies have not been observed in Ethela, but their apparent absence may not be inherent, but due to dissolution during fossilization. There are cyperaceous genera, however, that do lack silica bodies (e.g. Chorizandra Benth. & Hooker and Lepironia Rich.) (METCALFE 1971).

In Cyperaceae the median veins in leaves of certain genera are accompanied by a single abaxial strand or girder, plus additional abaxial strands to the right and left of the girder (METCALFE 1971). A similar arrangement is seen in Ethela in which a large vein (median bundle?) is flanked on each side by a smaller strand (Pl. IV, 3 Fig. 7, arrows). This feature is most common in the tribe Cypereae, within

Cyperus L., Pycreus Beauv., and Torulinium Desv. Other genera with this feature include: Bisboeckelera Kuntze (Sclerieae), Eriophorum L. (Scirpeae), and Fuirena Rottb. (Scirpeae) (METCALFE 1971). However, Ethela differs from these genera in details related to sclerenchyma shape, distribution, mesophyll differentiation, and bundle sheath structure.

Discussion

Based on leaf anatomy, Ethela is most similar to the Cyperaceae and Juncaceae. Because of the relatively close relationship between these two families it is not surprising that anatomically they are nearly identical and the few characters that separate them are those associated with reproductive structures (DAHLGREN & CLIFFORD 1982). Vegetative features such as the absence of silica bodies in Juncaceae have been noted as a distinction between the two families, but at least two cyperaceous genera lack silica bodies (METCALFE 1971). Silica bodies could have been present in Ethela but were dissolved away during silicification. As interpreted here, perforate tracheary elements occur in the roots and leaves. Perforate elements also occur in roots and leaves of the Cyperaceae and Juncaceae (DAHLGREN & CLIFFORD 1982).

Although it is generally agreed that the Cyperales (Cyperaceae) were derived from the Juncales (Juncaceae, Thurniaceae) (DAHLGREN & CLIFFORD 1982), the fossil record of the Juncaceae is poorly represented, whereas the Cyperaceae is well documented from Eocene and younger deposits throughout the world (DAGHLIAN 1981; MULLER 1981;

THOMASSON 1983; FRIIS 1985). On the other hand, the fossil record of Juncaceae extends only to the Lower Oligocene of Europe where it is represented by seeds (COLLINSON 1983). Most reports are from Miocene or younger sediments (DAGHLIAN 1981). These records are few and include one report of pollen from the Neogene of Russia (DAGHLIAN 1981), four reports of seeds from the Miocene of Europe (FRIIS 1985); and a megafossil, Juncus crassulus from the Lower Oligocene Florissant flora in Colorado (DAGHLIAN 1981).

Despite the wealth of information on anatomy of extant monocotyledons, care should be taken when using only vegetative characters to determine affinities of anatomically preserved fossil monocotyledons without knowledge of their corresponding reproductive organs. As shown here, Ethela shares features in common with several families and could easily be assigned to any one of them depending on what organs and which characters are used. Although culm-like axes, flowers, fruits, or seeds have not been found attached to or associated with the fossil stems, once this information is known a better understanding of the familial relationships of these plants will be possible. Until such time, the fossil plant is described here as a new taxon, Ethela sargantiana ERWIN & STOCKEY gen. et sp. nov., and assigned to the Commelinidae, family Incertae sedis.

Plate IV, 1 -

Ethela sargantiana gen. et sp. nov., stem anatomy.

Fig. 1. Cross section of stem (S) showing several sheathing leaves, leaf base (LB), and leaves punctured by diverging roots (R). — P1382 A1 #15 — 11x.

Fig. 2. Stem (S) cross section showing two small lateral branches (B) and roots (R). — P2561 Dtop #1 — 7x.

Fig. 3. Cross section of stem showing pith (P), central cylinder (CC), inner (IC) and outer (OC) cortex. Note primary thickening meristem at arrows. — P1328 G2bot #7 — 28x.

Fig. 4. Inner cortex showing large cells with dark contents that resemble tannin sacs. — P1130 A #4 — 90x.

Fig. 5. Branch cross section showing central cylinder, attached root, and remnants of scale-like leaves (arrow). — P2561 Dtop #1 — 27x.

Fig. 6. Cross section of inner cortex showing endodermal layer (EL) and radially aligned cells of primary thickening meristem. — P1328 G2bot #7 — 80x.

Fig. 7. Cross section showing cells of outer cortex and single-layered epidermis (E). Note dark contents in epidermal cells. — P1328 G2bot #8 — 160x.

Fig. 8. Cross section of central cylinder showing collateral (arrow) and amphivasal (arrowhead) bundles, phloem (PH), xylem (XY), and fibrous sheaths. — P1130 Dtop #26. — 60x

Fig. 9. Detail of vascular bundle from central cylinder showing fibrous bundle sheath (BS), phloem (PH), and xylem (XY). — P2561 Etop #0 — 220x.

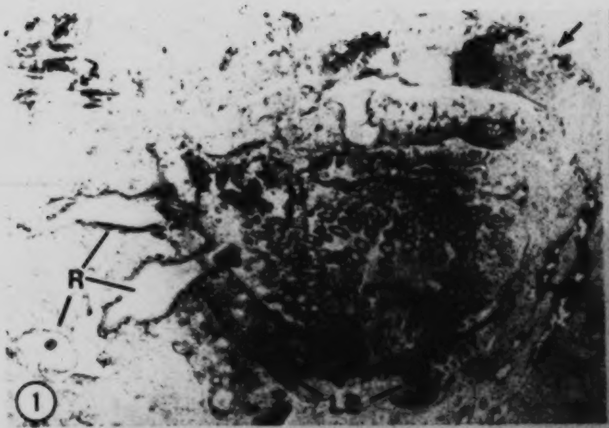
Fig.10. Longitudinal section showing tracheary element from stem with scalariform intervascular pitting (arrows). — P1328 G2bot #8 — 450x.

Fig.11. Longitudinal section showing thin-walled cells with dark contents associated with vascular tissues. — P1328 G2bot #7 — 260x.

Fig.12. Thick-walled pith cells. — P1328 G2bot #7 — 200x.

Fig.13. Tannin sac in pith. — P1328 G2bot #7 — 200x.

Fig.14. Cross section of inner cortex showing lobed cells and intercellular spaces (arrows), some filled with dark contents. — P1130 Ctop #1 — 200x.



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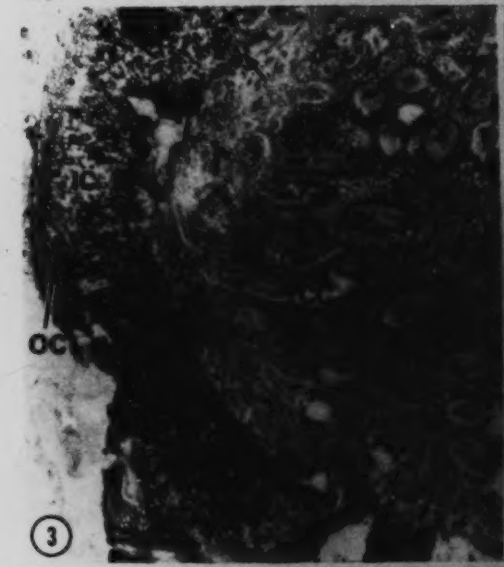

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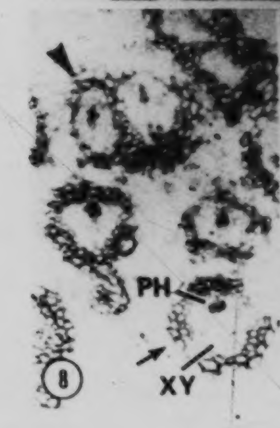

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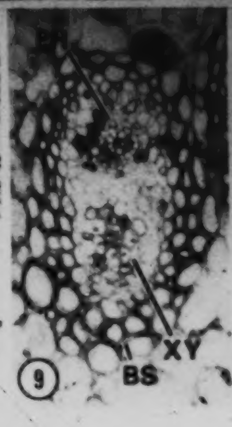

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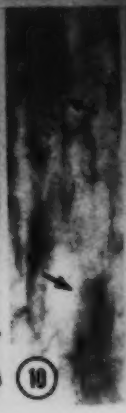

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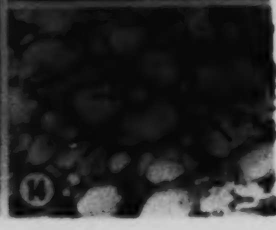

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Plate IV, 2

Ethela sargantiana. Stem and root anatomy.

Fig. 1. Root with solid cortex composed of square to rectangular cells in radial files. — P1328 G3Btop #1 — 12x.

Fig. 2. Cross section of root showing stele and poorly preserved cortex. — P1328 G2bot #1 — 100x.

Fig. 3. Cross section of stem showing diverging root trace (RT), central cylinder (CC), inner (IC) and outer (OC) cortex, and leaf trace (LT). Note continuation of endodermoid layer (arrows) with root endodermis. — 1328 G2bot #1 — 49x.

Fig. 4. Longitudinal section of root primordium showing root cap (RC) and epidermis (E). — P1328 G3top #1 — 96x.

Fig. 5. Stele showing xylem (XY) filled with dark contents and endodermis (EN). — P1328 G2bot #21 — 300x.

Fig. 6. Longitudinal section of vessel member with scalariform perforation plate (arrow). — P1328 G2bot #11 — 650x.

Fig. 7. Longitudinal section of vessel members with scalariform intervascular pitting and scalariform perforation plate (arrow). — P1328 G2bot #13 — 650x.

Fig. 8. Endodermoid layer (EL) that separating inner cortex (IC) and central cylinder (CC) showing cells with thick radial and inner tangential walls (arrows). — P1328 G3top #1 — 270x

Fig. 9. Cross section of root showing epidermis (E) and 2-3 layers of thick-walled hypodermis (H). — P1328 G2bot #1 — 260x.

①

RT
OC
LT
③

EN
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Plate IV, 3

Ethela sargantiana gen. et sp. nov., leaf anatomy.

Fig. 1. Stem (S) cross section with attached roots (R) and eight ensheathing leaves (1-8). — P1130 Ctop #23 — 12x.

Fig. 2. Proximal section of leaf showing collateral vein with bundle sheath (BS), phloem (PH), xylem (XY), associated fibrous strand (FS), tannin sacs (arrows), and possible stomatal apparatus (arrowhead). — P1328 G2bot #7 — 140x.

Fig. 3 Proximal cross section of leaves showing arrangement of veins (arrows) and abaxial fibrous strands. — P1130 Ctop #11 — 54x.

Fig. 4. Distal section of leaf showing distribution of veins primary fibrous strands and tannin sacs (arrows). — P1130 Dtop #26 — 140x.

Fig. 5. Abaxial epidermis showing fibrous strand and anticlinal walls. — P1130 Ctop #2 — 150x.

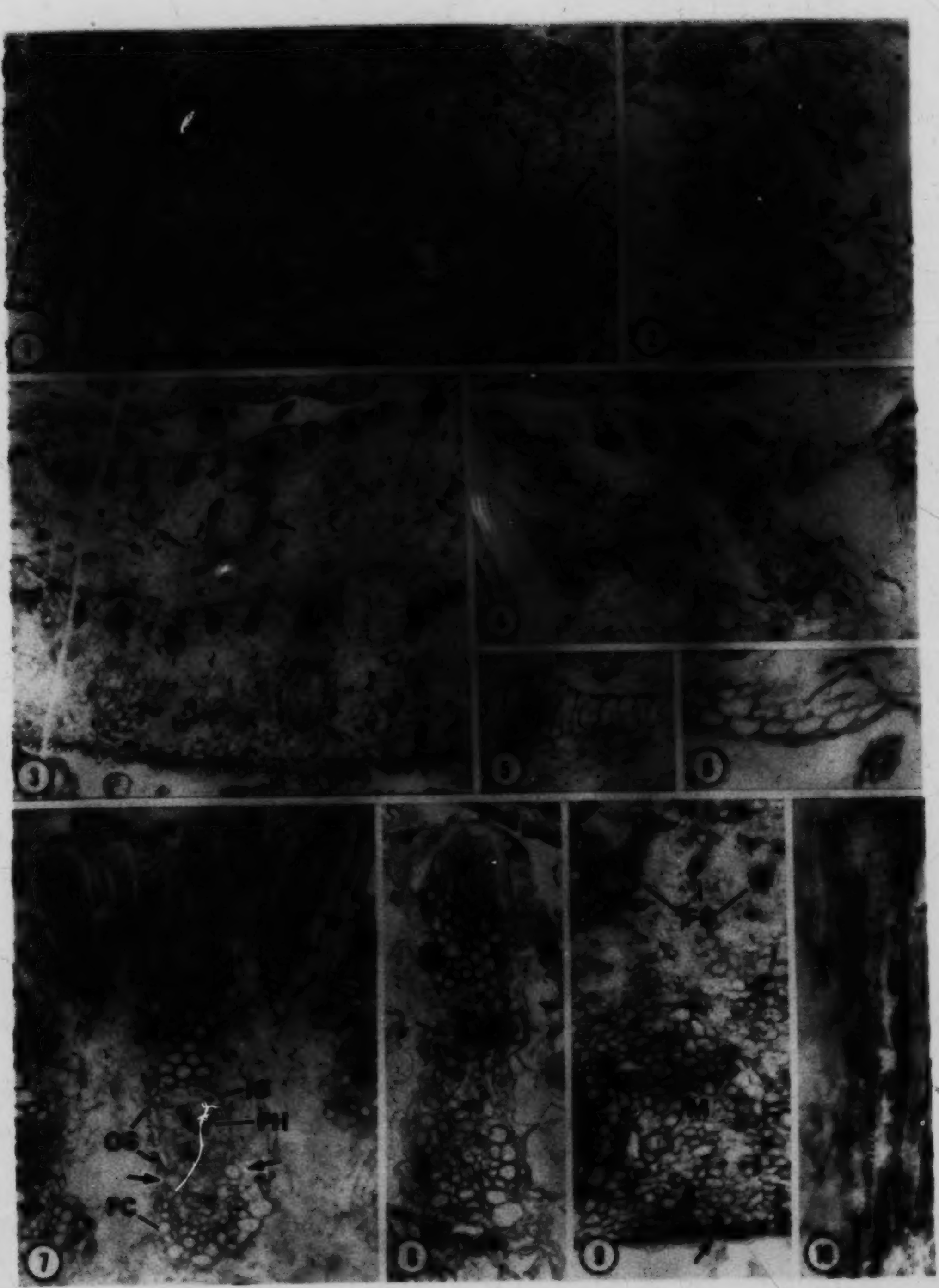
Fig. 6. Adaxial epidermis showing additional subepidermal layer. — P1130 Ctop #19 — 250x.

Fig. 7. Distal leaf section showing abaxial girder-like bundle sheath extension (G), phloem (PH), lateral narrow tracheary elements and associated smaller tracheary cells (arrows in lower half of photo), adaxial U-shaped fibrous cap (FC), primary fiber strands (arrowheads), and secondary fiber strands (arrows at top of photo). — P1130 A #4 — 170x.

Fig. 8. Cross section of major vein showing phloem cells (arrow) with dark contents. — P2561 Dtop #26 — 160x.

Fig. 9. Leaf cross section showing spongy mesophyll (M) fibrous strands (FS), and epidermal cell with dark contents (arrow). — P1382 A1 #17 — 79x.

Fig.10 Longitudinal section of tracheid showing scalariform intervascular pitting. — P1130 A #4 — 480x.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Chapter 5: *Soleredera rhizomorpha* gen. et sp. nov., a permineralized monocotyledon from the Middle Eocene Princeton chert of British Columbia, Canada.*

Introduction

Permineralized angiosperms are among the most abundant and diverse components of the Middle Eocene Princeton chert flora of southern British Columbia, Canada. Dicotyledon families such as the Lythraceae (CEVALLOS-FERRIZ and STOCKEY 1988a), Nymphaeaceae (CEVALLOS-FERRIZ and STOCKEY 1989), and Vitaceae (CEVALLOS-FERRIZ and STOCKEY 1990a) are known from fruits and seeds, while flower remains include descriptions of *Paleorosa similkameenensis* (Rosaceae) (BASINGER 1976a; 1976b) and *Princetonia allenbyensis* (*Incertae sedis*) (STOCKEY 1987). In addition, the families Rosaceae (CEVALLOS-FERRIZ 1989; CEVALLOS-FERRIZ and STOCKEY 1990c) and Magnoliaceae (CEVALLOS-FERRIZ and STOCKEY 1990b) are represented by numerous small twigs and larger stem fragments that share anatomical features with these taxa. Monocotyledons, on the other hand, are represented by abundant vegetative organs of a coryphoid palm (BASINGER 1976; ERWIN and STOCKEY 1987), araceous fruits and seeds referred to the extinct genus *Keratosperma* (CEVALLOS-FERRIZ and STOCKEY 1988b), and a small petiole, *Heleophyton helobioides* (ERWIN and STOCKEY 1989) that has structural characteristics consistent with petioles of the Alismataceae.

In this paper, we describe small monocotyledonous stems with lateral branches and numerous attached roots. The internal structure of the stems and roots is comparable to that found in several families of the Liliales. The megafossil record of Liliales extends back to the

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*A version of this chapter has been accepted for publication: Erwin & Stockey, 1990. Bot. Gaz. (in press).

Cretaceous and is based largely on reports of leaf compressions similar to those of the Smilacaceae and Dioscoreaceae (DAGHLIAN 1981). Dispersed pollen assignable to Liliacidites has been described; and although many of the grains assigned to this genus share similarities with pollen of the Liliaceae, this type of pollen is found in other monocotyledon families (DAGHLIAN 1981; MULLER 1981).

Material and methods

Monocotyledonous stems showing numerous vascular bundles scattered in lignified ground tissue have been identified in five chert blocks from the Princeton chert locality. The locality is part of the Allenby Formation that is exposed on the east bank of the Similkameen River, 8.4 km south of the town of Princeton, British Columbia. Chert deposits lie 650 m above the Princeton Black coal seam (BONEHAM 1968) and consist of 49 interbedded chert and coal layers with an occasional thin bed of ash (CEVALLOS-FERRIZ 1987). The site has been referred to as locality "I" (BONEHAM 1968) and the "Princeton chert" (BASINGER and ROTHWELL 1977; STOCKEY 1984). Based on K-Ar dating (HILLS AND BAADSGAARD 1967) and correlative studies of freshwater fish from equivalent aged strata (WILSON 1977, 1982), the Princeton chert has been dated Middle Eocene.

The specimens were studied using a modified acetate peel technique and hydrofluoric acid (BASINGER and ROTHWELL 1977; BASINGER 1981). Peel sections were mounted on microscope slides with either Coverbond or Eukitt xylene-soluble mounting medium for microscopic examination. Peels prepared for scanning electron microscopy were mounted on stubs with double-sided sticky tape, sputter-coated with 150 A Au on a Nanotek Sputter Coater, and examined with a Cambridge Stereoscan 250 at 20kV. All slides are housed in the University of Alberta Paleobotanical Collection (UAPC-ALTA).

Results

Systematic section

CLASS.—Liliopsida

SUBCLASS.—Liliidae

ORDER.—Liliales

FAMILY.—Incertae sedis

GENUS.—Soleredera gen. nov.

SPECIES.—Soleredera rhizomorpha sp. nov.

Diagnosis: Rhizomes and aerial stems. Rhizomes branched, herbaceous, maximum diameter 1.3 cm, length at least 3-4.5 cm; branches 2.0-3.0 mm wide, attached irregularly at different levels. Vascular bundles numerous, scattered, forming a central vascular cylinder; vascular plexus present in rhizomes. Pith hollow or parenchymatous. Rhizome vascular bundles primary, arranged in two or more irregular cycles; inner bundles of central cylinder collateral or amphivasal, outer bundles amphivasal. Aerial stem bundles primary, collateral, in 2-3 cycles; dimensions of bundles in cross section 0.15-0.30 mm radially X 0.12-0.24 mm tangentially. Metaxylem a U-shaped strand, 1-6 tracheids wide or sometimes more; tracheids angular, 9-42 um wide X 485-550 um long, with tapered overlapping end walls; intervascular pitting scalariform, transitional, opposite, or alternate; pits oval, angular, or tangentially elongate, bordered, vestured. Vestures knob or wart-like, lining inner wall of border adjacent to pit cavity, pit canal, and apertures. Protoxylem elements centrally located below curve of U-shaped metaxylem, 6-15 um wide, with annular to helical secondary wall thickenings. Phloem strand single, cylindrical, 30-46 um wide, located between arms of metaxylem. Phloem cells 6-18 um wide X 180-212 um long; sieve plates on transverse to slightly oblique end walls; lateral walls with sieve areas. Amphivasal bundles circular to oval in cross section,0.10-0.32 mm radially X 0.07-0.22 mm tangentially; xylem 1-4 layers of angular tracheary elements surrounding a central phloem strand; intervascular pitting mostly alternate; protoxylem elements not observed. Ground tissue mostly of compact, thin-walled parenchyma with simple pits, but also including scattered thick-walled sclereids with dark contents. Cortex 0.50 mm wide, vascular bundles absent. Epidermis one layer; cells rectangular in cross section, tangentially elongated. Exodermis one layer; cells square to rectangular, 21-45 um radially X 21-45 tangentially; radial and outer tangential walls dark, thick. Roots 0.5-1.5 mm wide, attached to all sides of stems, most numerous at levels of branching. Steles 0.1-0.8 mm wide, polyarch; protoxylem poles up to 20; wide vessels 30-45 um wide, with simple perforation plates.

Holotype: P2584 B, C; axis #1 (Fig. 1, axis on far right)

Paratypes: P1130 Ctop, Fbot; P1243 A-E; P2584 A, D, E; P5356 Bbot, C; P5881 D-I.

Etymology: Genus named for Dr. Hans Solereder in recognition of his contributions to our knowledge of monocotyledon anatomy. The specific epithet refers to the rhizomatous plant habit.

Description

GENERAL FEATURES

Soleredera is represented by 18 fragments of silicified, three-dimensionally preserved, monocotyledonous rhizomes and a half dozen aerial stems (Pl. V, 1 Figs. 1-3). Rhizomes are up to 1.3 cm in diameter (Pl. V, 1 Figs. 1-3, Pl. V, 2 Figs. 9-16) and the most complete specimen reaches a maximum length of ca. 4.5 cm. Aerial stems range in diameter from 6 mm to 1.0 cm. Most blocks of chert contain cross sections of single isolated rhizomes; in one slab a clump of seven branched plants were found (Pl. V, 1 Fig. 1, only 5 visible; arrows). The rhizomes in cross section show either a solid or hollow pith (Pl. V, 1 Figs. 1, 3, Pl. V, 2 Figs. 14, 15), whereas the pith in all the aerial stems is hollow (Pl. V, 2 Fig. 16). In both stem types the pith is surrounded by a vascular cylinder composed of numerous small vascular bundles scattered or arranged in two or more poorly defined cycles (Pl. V, 1 Figs. 1, 3, 4). External to the vascular cylinder is a parenchymatous cortex that is delimited from the central cylinder by the outermost vascular bundles and sometimes by the presence of an endodermoid layer (Pl. V, 1 Fig. 2, Pl. V, 4 Figs. 30, 31, 38). This layer is continuous with the endodermis of diverging roots (Pl. V, 1 Fig. 3). The roots are 0.5-1.5 mm wide, show typical monocot stelar organization, and represent several different developmental stages. In addition numerous roots of Soleredera are found isolated in the matrix (Pl. V, 1 Figs. 1-3).

RHIZOME MORPHOLOGY

Study of numerous serial peels shows rhizomes with lateral branches 2-3 mm wide (Pl. V, 1 Figs. 1, Pl. V, 2 Figs. 9, 12-15). The vegetative or fertile nature of these branches is not known. Branch histology is similar to the main stems, but the branches have fewer vascular bundles. The branching pattern is irregular. Branches arise from the rhizomes at different levels and the number of branches varies

(Pl. V, 1 Fig. 1, Pl. V, 2 Figs. 9, 12, 14). For example, Figures 9-13 represent consecutive proximal(?) sections through one rhizome fragment. At the level represented by Figure 9, two of three branches are attached while the third lies isolated in the matrix (arrow). The two attached branches are subopposite (Pl. V, 2 Fig. 9). In more proximal sections, the third branch ultimately becomes attached. This branch increases to a size equal to the main stem (Pl. V, 2, Figs. 10, 11) and eventually merges with it to form the large stem in Figure 13. Therefore, the third branch appears to be the result of a dichotomy or forking (Pl. V, 2 Fig. 12) of the larger stem in Figure 13 if the sections are traced distally. Although this one specimen suggests dichotomous branching, more specimens must be studied in order to confirm this interpretation. Dichotomous branching has been reported in several monocotyledons, e.g. Flagellaria (TOMLINSON 1970), Nypa (TOMLINSON 1971), and Hyphaene (TOMLINSON 1973). In addition, a smaller branch and incipient branch trace are attached to the larger stem in the most proximal section (Pl. V, 2 Figs. 12, 13). Roots appear to be produced along the entire length of the rhizomes and are not confined to nodes, but roots may be more abundant in nodal regions (Pl. V, 2 Fig. 15).

RHIZOME ANATOMY

In the rhizomes, bundles in the inner half to two-thirds of the vascular cylinder are collateral (Pl. V, 1 Figs. 4-6) whereas the more peripheral bundles are amphivasal and generally smaller than the collateral bundles (Pl. V, 1 Figs. 4, 7, 8, Pl. V, 4 Fig. 30). In still other rhizomes all or most of the bundles are amphivasal (Pl. V, 2 Figs. 10-12).

Collateral bundles in cross section range in diameter from 0.07-0.22 mm wide to 0.15-0.30 mm long (Pl. V, 1 Figs. 5, 6). In one specimen, a sheath of narrow thick-walled fibers surround the bundles (Pl. V, 1 Fig. 6) whereas in other specimens, only the phloem has a fibrous sheath (Pl. V, 1 Fig. 5). Metaxylem in collateral bundles forms a U or V-shaped strand composed of up to 6 layers or more of angular tracheary elements with several narrow protoxylem elements centrally located just below the curve of the metaxylem (Pl. V, 1 Figs. 5, 6). In longitudinal section, protoxylem elements show annular to helical secondary wall thickenings (Pl. V, 3 Figs. 20, 21). Metaxylem elements are angular in cross section (Pl. V, 1 Figs. 5, 6), 9-42 um wide X 485-550 um long, have tapered end walls, and appear to be tracheids rather than vessels (Pl. V, 3 Fig. 22). Lateral wall pitting among the trachery elements range from scalariform (Pl. V, 3 Fig. 21), transitional (Pl. V, 3 Fig. 23), opposite, or alternate (Pl. V, 3 Fig. 22). The pits are oval, transversely elongated, or angular (Pl. V, 3 Figs. 22, 23).

Warty protuberances occur in association with the apertures and give the pits a vestured appearance (Pl. V, 3 Figs. 27, 29). For example, Figure 27 represents a section of the inside wall of a tracheary element taken from the rhizome. On the right side of Figure 27, secondary wall is preserved along with vesture-like structures that appear to be direct extensions from the secondary wall that surrounds the apertures (arrows). Many of these outgrowths extend into and occlude the pit openings (Pl. V, 3 Figs. 27, 29). Figure 49A is a schematic drawing of a bordered pit pair in cross section showing the attachment of these projections to the secondary wall as seen in Figure 27. By contrast, the single file of raised oval structures (Pl. V, 3 Fig. 27, at left) are casts of the pit cavities left behind after removal of the secondary wall (Pl. V, 6 Fig. 49B). Similar casts are shown in more detail in Figure 28 along with possible remnants of the primary wall. In both Figures 27 and 28, the casts have a perforated appearance. Clorer examination shows that some of the perforations near the central area where the aperture would be are three dimensional, hollow structures (Pl. V, 3 Fig. 28, arrow). A possible explanation or interpretation for these and the perforations is that they represent "molds" of the vesture-like extensions that once extended into the pit cavity (Pl. V, 6 Fig. 49 A&B).

Pseudovestures or incrustations formed by the deposition of secondary plant products in the tracheary elements can be and have been mistaken for true vestures (WHEELER 1981; GALE 1982). According to WHEELER et al. (1989), treatment of wood with bleach apparently dissolves these deposits. Since the fossil material can not be bleached, it is not possible to definitely state that the fossil pits are vestured.

Each vascular bundle has a single phloem strand located between the arms of the metaxylem and capped by several layers of thin- to thick-walled fibers (Pl. V, 1 Figs. 5, 6). In cross section, phloem cells are 6-18 um in diameter. Sieve tube elements are difficult to distinguish from companion or parenchyma cells in cross section, but in longitudinal section sieve tube elements show sieve plates on transverse to slightly oblique end walls and sieve areas on the lateral walls (Pl. V, 3 Figs. 17-19). In some specimens, phloem is not preserved and is represented by a lacuna (Pl. V, 1 Fig. 6). Included in the phloem of some bundles are thick-walled cells (Pl. V, 1 Fig. 7).

Amphivasal bundles in cross section are circular to oval, vary in size from 0.10-0.30 mm radially X 0.07-0.22 mm tangentially, and show a central phloem strand surrounded by 1-4 layers of angular metaxylem elements similar to those found in the collateral bundles (Pl. V, 1 Figs. 7, 8). Lateral wall pitting of the metaxylem elements is mostly alternate. Protoxylem elements have not been observed in these bundles. Sieve tube elements are shorter, but are similar to those in the collateral bundles. For the most part, amphivasal bundles occur singly (Pl. V, 1 Fig. 4, Pl. V, 4 Fig. 30); but throughout the outer vascular cylinder, occasionally two, three, or more bundles are confluent (Pl. V, 1 Fig. 8).

The amphivasal bundles at first were interpreted to be secondary in origin, rather than primary. In several specimens, near the periphery of the vascular cylinder there is a layer 1-2 cells wide with thin to thick cell walls (Pl. V, 4, Figs. 30, 31). The vascular bundles lying beneath this layer have the appearance of being in a young stage of development (Pl. V, 4 Figs. 30, 31), and in several places at the periphery of the central cylinder, the vascular bundles seem to be radially aligned (Pl. V, 4 Fig. 30). However, cells of the ground tissue are not radially arranged (figs. 30, 31) and there is no radial sertion of parenchyma on the outer side of the putative cambial zone (ESAU 1977). Furthermore, very few cells in this layer show periclinal divisions suggestive of a true cambial layer and the thick-walled nature of the cells is more indicative of an endodermoid or sclerotic layer than a vascular cambium. In some stem cross sections, a relatively wide vascular plexus composed of numerous tracheary elements with occasionally interspersed phloem strands occurs just to the inside of the endodermoid layer (Pl. V, 4 Fig. 36). The vascular tissues are seen in longitudinal section, and in serial peels they eventually diverge as lateral branch traces. Tracheary elements are sinuous, they vary in length and width, and some are irregularly shaped (Pl. V, 4 Figs. 32, 35). Although a few of the elements appear to be vessels with simple perforations, closer examination shows the perforations to be spaces (pseudoperforations) (Pl. V, 4 Fig. 33) that form in areas where two or three elements meet along their lateral walls (Pl. V, 4 Fig. 34). Only tracheids have been observed in the branches.

Ground tissue of the pith, central vascular cylinder, and cortex is composed of compact lignified parenchyma with small intercellular spaces (Pl. V, 1 Figs. 4, Pl. V, 4 Figs. 30, 39). Cells in cross section are polygonal, have relatively thin-walled, and generally decrease in diameter toward the stem periphery (Pl. V, 1 Fig. 4, Pl. V, 3 Fig. 25). In longitudinal section, ground tissue cells are square, rectangular, or elongate and tabular, with walls that show numerous simple pits (Pl. V, 4 Figs. 37, 39). The amount of cell wall is variable. Ground parenchyma of some specimens shows relatively thick secondary walls (Pl. V, 1 Fig. 6), while in others it has thinner walls. Included in the ground tissue are very thick-walled, pitted sclereids with dark contents (Pl. V, 4 Fig. 37) These cells are most common in the cortex and outer regions of the central cylinder near areas of root insertion.

The cortex is narrow, 0.50 mm wide, and lacks vascular bundles (Pl. V, 4 Fig. 38). Surrounding the cortex is a single-layered epidermis composed of thin-walled rectangular, tangentially elongated cells (Pl. V, 4 Fig. 38). A cuticle has not been observed. Remnants of septate fungal hyphae are present throughout the ground tissue, being particularly abundant in pith and cortical cells (Pl. V, 4 Fig. 40). The presence of dark contents in some of the ground tissue cells could possibly be the result of fungal activity; however, some of the contents may represent tannin deposits.

AERIAL STEM ANATOMY

Associated with the branched stems illustrated in Figure 1 is a laterally compressed axis that is 1.0 cm wide, shows a hollow pith surrounded by a central vascular cylinder, and lacks a cortex (Pl. V, 2 Fig. 16). In addition to this specimen, there are several other smaller stems of this same type in two different chert blocks. Amphivasal bundles are absent from the central cylinder of these stems, but otherwise the vascular system closely resembles that of the inner cycles of collateral bundles in the rhizomes (Pl. V, 1 Fig. 6, Pl. V, 2 Figs. 14, 15). For example, bundle structure and ground tissue in these stems (Pl. V, 3 Fig. 24) is nearly identical to these same tissues in the rhizomes (Pl. V, 1 Fig. 6).

In longitudinal section, the tracheary elements show helical to scalariform lateral wall thickenings, but the phloem is not preserved and is represented only by lacunae (Pl. V, 3 Fig. 24). Ground tissue consists of lignified thin-walled parenchyma with relatively large intercellular spaces (Pl. V, 3 Fig. 24). Based on its histological similarities to the rhizomes, its close association with the rhizomes, and its lack of attached or associated roots, this axis probably represents a portion of an aerial stem (culm).

ROOT ANATOMY

In cross section, steles are 0.1-0.8 mm wide, cylindrical, medullated, and polyarch with up to 20 protoxylem poles in the largest roots (Pl. V, 5 Figs. 42, 43). Each xylem strand is 1-2 cells wide and consists of a radial series of angular tracheary elements that decrease in diameter toward the protoxylem poles (Pl. V, 5 Figs. 43, 45). In some steles, the xylem strands join to form U-shaped bands that overarch individual phloem strands (Pl. V, 5 Figs. 43, 45). The largest tracheary elements are vessels, 30-45 um wide, that in longitudinal section show simple perforation plates on oblique end walls (Pl. V, 5 Figs. 47, 48). Intervascular pitting is mostly alternate (Pl. V, 5 Fig. 48).

Circular to oval phloem strands alternate with the xylem (Pl. V, 5 Figs. 42-45). Phloem is usually not preserved but is represented by lacunae. Therefore, the steles appear at low magnification appear to have a single ring of wide vessels (Pl. V, 5 Fig. 42). External to the vascular tissues is a one- to two-layered pericycle (Pl. V, 5 Fig. 45). Pericycle cells in cross section are thick-walled and generally larger than the internal ground tissue fibers associated with the vascular tissues, but in many cases the two are difficult to distinguish.

Surrounding the vascular cylinder is a single-layered endodermis (Pl. V, 5 Figs. 43, 45). Cells of the endodermis show thickened radial and inner tangential walls, which give the cells a U-shaped appearance in cross section (Pl. V, 5 Figs. 43, 45). Located opposite the xylem strands are thin-walled passage cells that occasionally occur in place of the thicker walled endodermal cells (Pl. V, 5 Figs. 43, 45). In longitudinal section, cells of the endodermis are axially elongated and have scalariform-like pitting on the inner tangential walls (Pl. V, 6 Fig. 46).

The pith and cortex consist of compact thin-walled parenchyma similar to that composing the stem ground tissue (Pl. V, 5 Figs. 41, 42, 44). However, the degree of sclerification of the pith cells is variable among different root specimens of Soleredera. In living monocotyledons this difference in the amount of cell wall is a direct function of age (TOMLINSON 1961) whereby older roots typically having a more sclerotic pith.

Cells of the pith are generally thinner-walled, more polygonal, and wider than the adjacent fibrous ground tissue associated with the vascular tissues (Pl. V, 5 Figs. 43, 44). The fibrous ground tissue consists of thick-walled, narrow fibers that are more or less circular in cross section (Pl. V, 5 Figs. 43-45).

The cortex in most roots is not preserved, but is represented only by space (Pl. V, 2 Figs. 10, 15, Pl. V, 5 Figs. 41-43). In root cross sections taken near the point of attachment, the cortex consists of compact, relatively thin-walled lignified parenchyma with little intercellular space (Pl. V, 5 Fig. 44). Epidermal cells in cross section are relatively large and square to subrectangular (Pl. V, 5 Figs. 42, 43). Lying below the epidermis is a single layer of smaller cells that may represent the exodermis (Pl. V, 5 Fig. 42). In attached and isolated roots the epidermis is usually the only layer preserved, but occasionally remnants of the exodermis can be seen (Pl. V, 5 Fig. 43).

Discussion

Unlike stems of woody dicotyledons, stems of monocotyledons often lack diagnostic anatomical characters that can readily identify them to a genus or family because of the high degree of structural conservatism demonstrated by these organs. There are a few exceptions however, for example, palm stems (TOMLINSON 1961) and those of Dioscoreaceae (AYENSU 1972; AL-SHEHBAZARD and SCHUBERT 1989) are anatomically distinct and can be identified to family.

Within the past 60 years a large amount of data has been compiled documenting the vegetative anatomy of monocotyledons (e.g., SOLEREDER and MEYER 1928, 1930, 1933; CHEADLE and UHL 1948; FAHN 1953, 1954; METCALFE 1960, 1971; TOMLINSON 1961, 1969, 1982; CARLQUIST 1966; CUTLER 1969; AYENSU 1972; DAGHLGREN and CLIFFORD 1982). However, because descriptions of extant monocotyledons are based on sections taken from a specific level of mature plant organs, it is often impossible to know if the fossil and extant sections represent comparable levels. Also, in most studies, changes in anatomy from one level to another within a single plant organ are difficult to document and therefore not included. Furthermore, rhizomes, corms, and bulbs are sometimes described but often are not illustrated. Despite these limitations, structural characters such as morphology of vascular bundles, presence or absence of vessels, degree of vessel end wall specialization, distribution of vessels in plant organs, and systematic distribution of vessels have been recorded for numerous monocotyledonous families and are considered to be taxonomically important (DAGHLGREN and CLIFFORD 1982; DAGHLGREN and RASMUSSEN 1983).

The tracheary elements in the stems of Soleredera are interpreted as tracheids whereas vessel elements with simple perforations occur in the roots. Extant monocot taxa that combine these features include the Restionales (Restionaceae), Bromeliales, Commeliniales (Cartonemataceae), Zingiberales, Alismatales, and Liliales. Many of these taxa, however, can be eliminated based on other differences in stem and root anatomy.

The central cylinder in the rhizomes of Restionaceae has amphivasal bundles, but the smaller peripheral bundles are collateral in some species (CUTLER 1969). In the fossil rhizomes, peripheral bundles are amphivasal and most collateral bundles are located internally. Tracheary elements in the rhizomes of Restionaceae include narrow vessels with simple perforation plates on nearly transverse end walls and show scalariform lateral wall pitting (CUTLER 1969). By contrast, tracheary elements in Soleredera are tracheids with mostly alternate intervascular pitting. In addition, aerial stems of Restionaceae show one to several layers of palisade-like chlorenchyma cells with lateral peg-like projections, a parenchyma sheath that borders on the chlorenchyma, and an internal sclerenchyma sheath that completely encircles the central cylinder and in which are embedded the peripheral vascular bundles (CUTLER 1969). Also the vascular bundles in the aerial stems are surrounded by a fibrous bundle sheath (CUTLER 1969).

In the genera of Bromeliales studied thus far, only two have roots with simple perforations, Pitcairnia and Vriesea, but both have vessel elements in the stems (WAGNER 1977). Likewise, in the Commeliniales, the Cartonemataceae have simple perforations in the roots and tracheids in the stems; but according to PICHON (1946) there are vascular bundles in the stem cortex, a feature not observed in Soleredera.

Within Zingiberales there are five families that show similarities in type and distribution of tracheal elements to those of Soleredera: Zingiberaceae, Musaceae, Strelitziaceae, Marantaceae, and Cannaceae. The rhizomes and aerial stems of the Zingiberaceae differ from those of Soleredera in several features. Rhizomes of Zingiberaceae show a relatively wide cortex that includes vascular bundles with massive fibrous sheaths (TOMLINSON 1969). Likewise, the aerial stems display a cortex containing one or more cycles of vascular bundles, and each bundle has a fibrous sheath (TOMLINSON 1969).

Plants in Musaceae are large herbs with cormous stems that possess vascular bundles surrounded by a fibrous sheath (TOMLINSON 1969). Articulated laticifers are common next to the vascular bundles in all plant parts except the roots, and raphide sacs are found in all plant organs (TOMLINSON 1969). Roots of Musaceae have an anomalous stelar organization in which numerous wide vessels and individual phloem islands are scattered throughout the central ground tissue (RIOPEL and STEEVES 1964; TOMLINSON 1969). These features are unlike the typical polyarch steles in the roots of Soleredera.

The Strelitziaceae is a small family containing three genera, however, only the genus Phenakospermum has simple perforations in the roots, but the stems are woody and have vessels (TOMLINSON 1969).

Unlike Soleredera, rhizomes in the Marantaceae have a cortex with numerous peripheral fibrous strands and vascular bundles. The vascular bundles in the central cylinder of most genera of Marantaceae are surrounded by a well-developed fibrous sheath opposite the xylem pole only (TOMLINSON 1969).

The Cannaceae have rhizomes and aerial stems with conspicuous mucilage canals in the cortex and periphery of the central cylinder. In the aerial stems, the peripheral vascular bundles have well developed fibrous sheaths and together with fibrous strands form a weak mechanical zone (TOMLINSON 1969). Also, roots of Cannaceae lack a pith (TOMLINSON 1969) while those of Soleredera have a conspicuous pith.

Tracheids in the rhizomes and aerial stems of the Alismatales have double spiral thickenings or scalariform pitting on the lateral walls (STANT 1964), while tracheid pitting in Soleredera is alternate. Roots of several taxa in the Alismatales have vessels with simple perforations, but the steles are characterized by a single, centrally-located wide metaxylem vessel surrounded by a variable number of peripheral protoxylem poles (TOMLINSON 1982). Some roots have a typical polyarch structure, but also possess a central vessel. The central vessel appears to be a consistent feature in roots of Alismatales (STANT 1964; TOMLINSON 1982) but one not found in the fossil.

Soleredera compares most favorably to families in the Liliales with respect to tracheary elements, as well as aspects of stem and root anatomy. Following the circumscription of Liliales sensu CRONQUIST (1988) (see DAGHLGREN and CLIFFORD 1982 and DAGHLGREN 1989 for an alternative classification), those families with tracheids in the stems and vessels with simple perforations in the roots include Agavaceae, Haemodoraceae (Conostylidaceae), Iridaceae, Liliaceae (including the segregate families Alliaceae, Alstroemeriaceae, Aphyllanthaceae, Asphodelaceae, Convallariaceae, Dianellaceae, Hyacinathaceae, Philesiaceae, Velloziaceae, and Xanthorrhoeaceae, sensu Cronquist, 1988).

Within Liliaceae, the Aphyllanthaceae, Velloziaceae, and Xanthorrhoeaceae differ from the fossil in stem structure. According to TOMLINSON (1964), rhizomes of Aphyllanthes (Aphyllanthaceae) show evidence of secondary growth, and both the primary and secondary bundles are always amphivasal. Plants in Philesciaceae are woody shrubs, undershrubs, tall climbers, or epiphytes (HUTCHISON 1973). Stems of Velloziaceae have been described as erect and dichotomously branched (HOLM 1895). Anatomically they differ from Soleredera in having sclerenchyma bands in the cortex that alternate with the vascular bundles in this region (AYENSU 1968). Also, the vascular bundles are all collateral and have a V-shaped fibrous sheath next to the xylem (AYENSU 1968). The stems (rhizomes) of Xanthorrhoeaceae are unlike the fossil in that many of them have a wide cambial zone, bundles with well developed fibrous sheaths, ground tissue with raphides or druses, and a central cylinder with an outer zone of up to 8 layers of fibers surrounding the central parenchyma (FAHN 1953).

Once more is known about stem (rhizome) anatomy in extant genera of these families as well as fossil leaf and floral parts of *Soleredera*, a more refined taxonomic treatment of the fossil will be possible. Although the fossil stems have structural features in common with the lilialean families listed above, there are no distinguishing features to support its placement in one specific family. Therefore, a new genus and species, *Soleredera rhizomorpha* gen. et sp. nov. Erwin et Stockey, is proposed for the Princeton stems.

The finding of putative vestured pits in the tracheary elements of *Soleredera* is, to our knowledge, the first report of such pit ornamentation in monocotyledons, despite the tremendous amount of research that has been done characterizing the tracheary elements in this group of plants (CHEADLE 1942, 1943b, 1943b, 1944, 1955, 1963, 1968, 1969, 1970, 1987; CHEADLE and KOSAKI 1971, 1972, 1973, 1975; CHEADLE et al. 1988, 1989; FAHN 1954; KLOTZ 1977, 1978). Using light microscopy, these structures were first recognized by RECORD (1925) as "cribiform membranes" in dicot vessels. BAILEY (1933) later suggested the descriptive term "vestured" for pits with cell wall outgrowths.

Vestures are described as wart-like, knob-like, or minutely dendriform projections from the secondary cell wall that wholly or partially cover the inside surface of the border, pit canal, and aperture (CARLQUIST 1988; WHEELER et al. 1989; NAIR and MOHAN RAM 1989). Vestured pits are most commonly found in certain families of dicotyledons (METCALFE and CHALK 1985; CARLQUIST 1988; NAIR and MOHAN RAM 1989) but have never been reported in tracheary elements of monocotyledons. Subsequent studies have shown that vestures are not restricted to pits of dicot vessels, but also occur in axial parenchyma (OHTANI 1986), interfiber pits (OHTANI 1987), intertracheid pits of both dicots and conifers (CARLQUIST 1988; WHEELER et al. 1989), and tracheoid cells in the seeds of papilionoid legumes (LERSTEN 1982). Furthermore, vestures are not exclusively found in pits, but occur on the inner surface of vessels and tracheids. These occurrences therefore suggest the independent origin of this character in these two widely divergent groups of plants and one not restricted to secondary xylem. Therefore, the apparent absence of this feature in monocotyledons is somewhat puzzling and one that seems to warrant further investigation in light of the discovery of vesture-like structures associated with the pits of Soleredera.

Both the megafossil and palynological record of the Liliales is poorly known (DAGHLIAN 1981; MULLER 1981). Leaf compressions ranging in age from the Late Cretaceous (Maastrichtian) to Early Oligocene have been assigned to the form genus Haemanthophyllum Budantsev. This genus includes both cordate and ribbon-like leaves and has been assigned to the Liliales (BOULTER and KVACEK 1989). The ribbon-like leaves were formerly referred to extant genera such as Potamogeton and Alisma. However, Haemanthophyllum shows more features in common with Amaryllidaceae and Aponogetonaceae (GOLOVNEVA 1987), but cannot be assigned to either family with certainty. Additional leaf compressions resembling Smilacaceae and Dioscoreaceae have been described, but the affinities of these fossils are dubious and need reinvestigation (DAGHLIAN 1981). A more reliable record of Liliales comes from a recent report of fossil Smilax (Smilacaceae) leaves from the Middle

Eocene of Tennessee (SUN and DILCHER 1988). Cuticular features and fine venation patterns of these fossil leaves are nearly identical to those of modern Smilax species.

The Agavaceae is represented by permineralized remains of a Yucca-like plant described as Protoyucca shadishii TIDWELL and PARKER (1990) from Miocene deposits in Nevada. Protoyucca is a large arborescent monocot with secondary growth that is similar to extant Yucca in stem anatomy, but differs from modern Yucca with respect to leaf and root anatomy (TIDWELL and PARKER 1990). This plant differs from Soleredera in having an arborescent growth habit characterized by secondary growth as well as in primary vascular bundle morphology and root anatomy.

The earliest record of pollen is that of the genus Astelia (Liliaceae) from Upper Eocene sediments of New Zealand (MILDENHALL 1980). Grains similar to Phormium (Agavaceae) are also known from the Middle to Upper Eocene of New Zealand (MULLER 1981). Smilax pollen postdates the megafossil record, being first recognized in the Upper Miocene (MULLER 1981). Pollen of Liliaceae, Agavaceae, Amaryllidaceae, Dioscoreaceae, and Iridaceae have been reported from Cretaceous and younger deposits, but are considered "pending" until further documented (MULLER 1981).

Soleredera represents the first anatomically preserved fossil monocotyledon with lilialean affinities to be described from the Middle Eocene of western North America. The exquisite internal preservation has allowed its comparison to extant monocotyledons, but for lack of fossil leaf anatomy and reproductive organs, assignment of Soleredera to a family is not possible at this time. However, continued study of the Princeton chert should yield both the foliage and reproductive organs necessary to fully reconstruct this early Tertiary monocotyledon.

Plate V, 1

Soleredera rhizomorpha gen. et sp. nov. rhizome anatomy.

Fig. 1. Cross sections of several associated plants (arrows) showing branches and attached roots. Holotype specimen at right. P2584 B bot #2 x 3.2.

Fig. 2. Cross section at level showing solid pith (p). P2584 C bot #3 x 8.5.

Fig. 3. Cross section showing hollow pith, central vascular cylinder (cc) with numerous scattered bundles (arrows), and attached roots (r). P2584 C top #3. X 7.5.

Fig. 4. Central vascular cylinder showing inner collateral bundles (lower half of figure) and outer amphivasal bundles (upper half of figure). P2584 B bot #1 x 60.

Fig. 5. Collateral bundle showing phloem (ph), phloem fibers (pf), U-shaped metaxylem (mx), and protoxylem (px). P1243 D2 top #8 x 130.

Fig. 6. Collateral bundles with fibrous sheath (at f) and nonpreserved phloem (arrow). Note thick-walled ground tissue and intercellular spaces. P1243 C2 top #8 x 95.

Fig. 7. Amphivasal bundle showing central phloem strand (ph) surrounded by xylem (xy) and thick-walled cells (arrow). P2584 B bot #14 x 200.

Fig. 8. Two fused bundles in periphery of central cylinder and narrow fibers at margin of the xylem (arrows). P2584 B bot #14 x 130.

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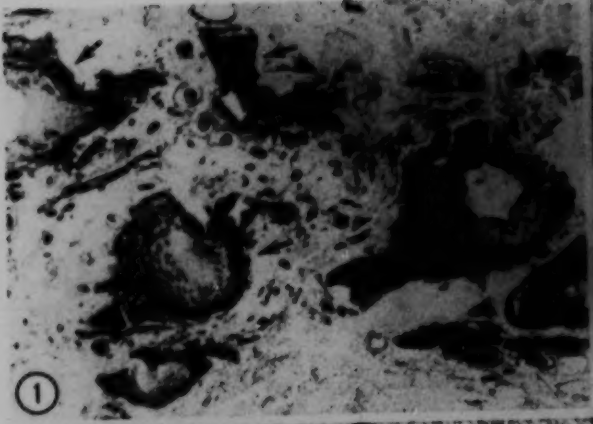
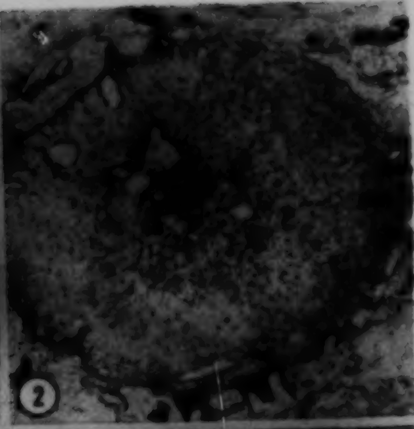
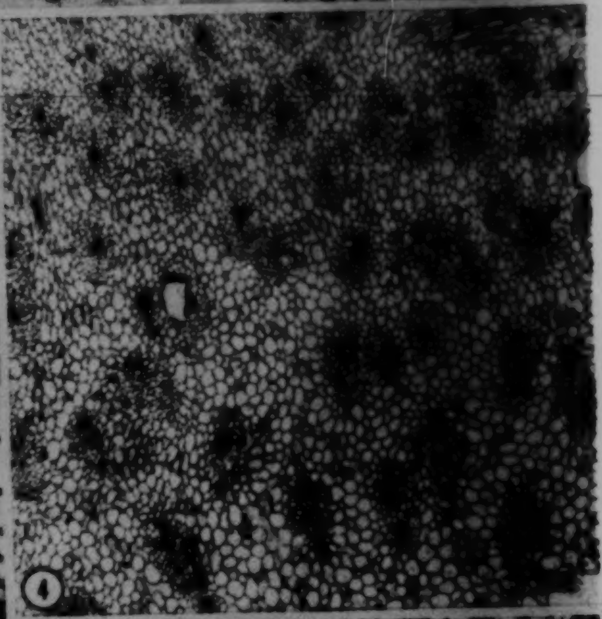
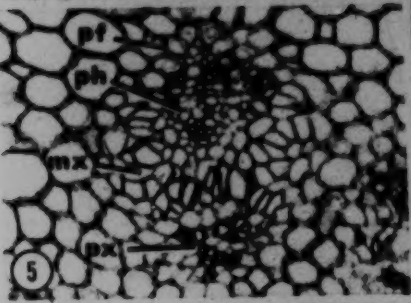
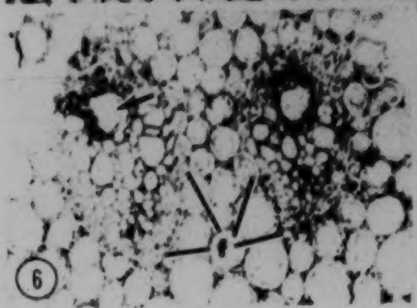
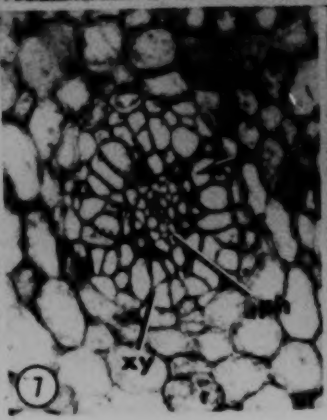












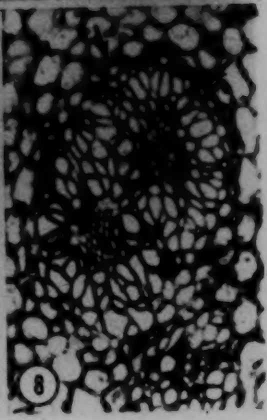


Plate V, 2

Solleredera rhizomorpha gen. et sp. nov. rhizome and aerial stem.

Fig. 9. Cross section of rhizome at distal level showing two attached branches and a third isolated in the matrix (arrow). P2584 C top #21 x 4.5.

Fig. 10. Consecutive level at which small branch (arrow) is nearly equal in size to that of the main stem. P2584 C top #48 x 11.

Fig. 11. Large and small branch (arrow) attached in area of diverging roots (at left). P2584 C top #49 x 11.

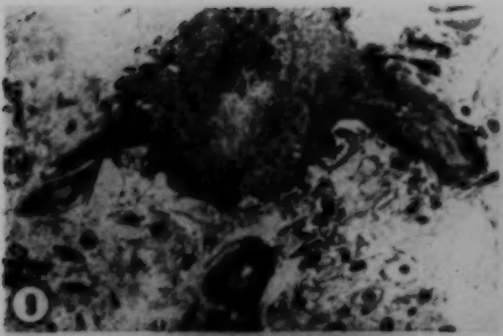
Fig. 12. Proximal level at which large and small branch merge into one stem. Note small lateral branch (b) and incipient branch trace (bt). P2584 C top #55 x 11.

Fig. 13. Most proximal level showing oblique section of large stem with smaller branch. P2584 C top #59 x 9.

Fig. 14. Distal section showing lateral branch and aerial stem. P2584 C bot #55 x 9.

Fig. 15. Proximal section of rhizome in fig. 14 at a level transitional to the aerial stem showing diverging branch (upper left) and numerous roots. P2584 C bot #44 x 9.

Fig. 16. Cross section of associated aerial stem showing hollow pith and 2-3 cycles of collateral bundles. P2584 B bot #20 x 8.5.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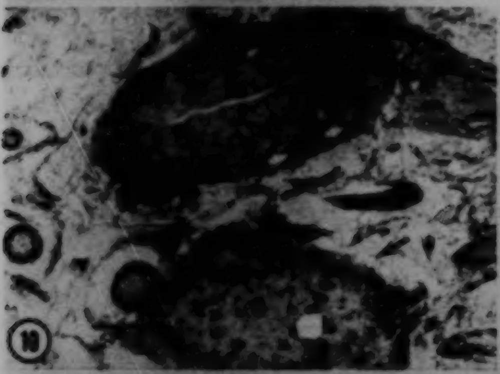
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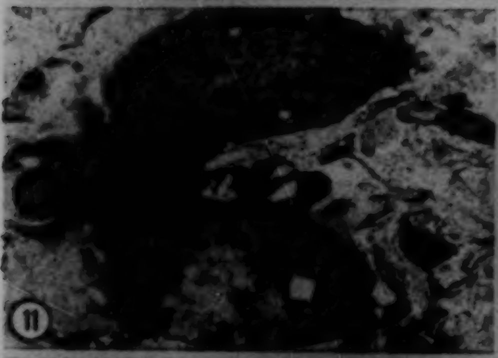
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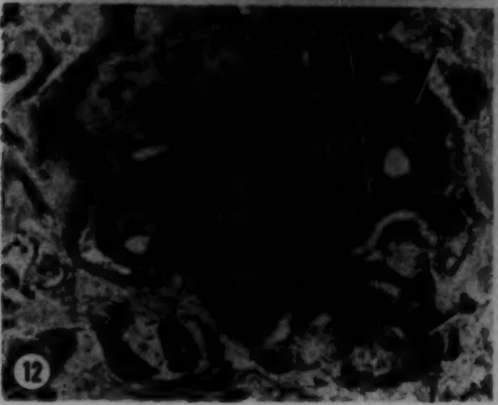
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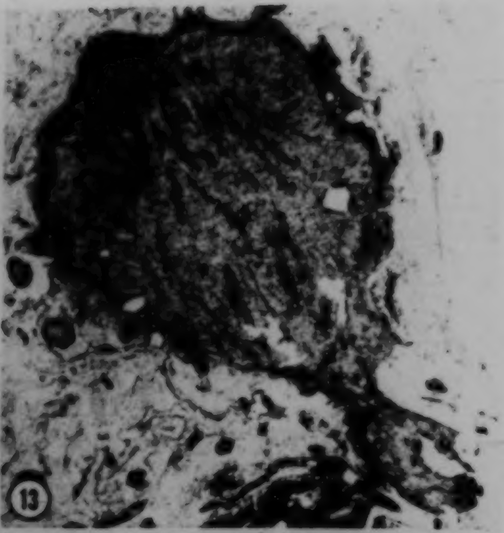
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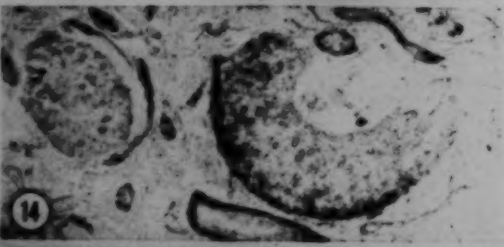
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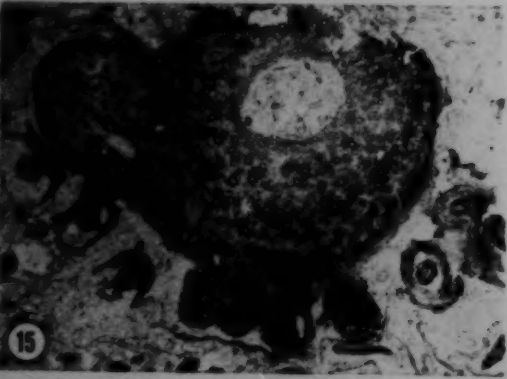
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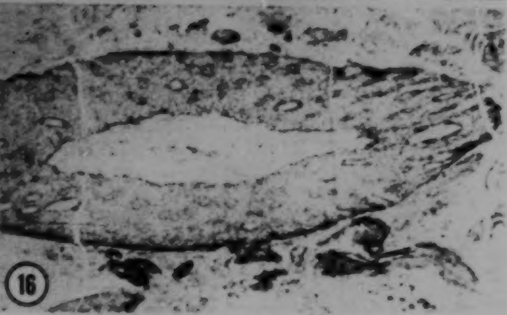
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Plate V, 3

Soleredera rhizomorpha gen. et sp. nov., vascular tissues.

Fig. 17. Longitudinal section showing portions ofsieve tubes (st). Xylem (xy) at left. P2584 C bot #3 x 230.

Fig. 18. Detail of sieve plates showing pores (arrows). P1243 D top #8 x 500.

Fig. 19. Sieve tube element showing lateral sieve areas (arrows). P2584 D top #7 x 580.

Fig. 20. Protoxylem elements showing annular and helical secondary wall thickenings. P2584 C top #18 x 300.

Fig. 21. Longitudinal section of protoxylem (left) and early metaxylem showing scalariform lateral wall pitting. P2584 B bot #5 x 450.

Fig. 22. Tracheids from rhizome showing alternate intervascular pitting and tapered overlapping end walls. P2584 B bot #13 x 270.

Fig. 23. Tracheid from lateral branch showing transitional intervascular pitting. P2584 B bot #10 x 950.

Fig. 24. Cross section of collateral bundle from aerial stem showing V-shaped xylem strand (xy), phloem (ph) lacuna and fibers (pf). P2003 B top #0 x 120.

Fig. 25. Tracheary element from aerial stem showing scalariform wall pitting. P2706 C top #0 x 220.

Fig. 26, Longitudinal section of narrow fibers associated with the xylem of amphivasal bundles showing circular to elliptical pitting. P2584 B bot #5 x 330.

Fig. 27. Inside wall of a tracheary element showing a single file of pit cavity casts (left) and remains of secondary wall (sw), apertures, and vesture-like projections (arrows). P2584 B bot #7 x 4000.

Fig. 28. Detail of pit cavity casts and remnants of primary wall (pw). Note perforated appearance of pit cavity cast possibly due to removal of vestures and hollow knob-like structures (arrow). P2584 B bot #7 x 9000.

Fig. 29. Apertures (ap) with wart-like projections. P2584 B bot #3 x 13000.

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Plate V, 4

Soleredera rhizomorpha gen. et sp. nov., stem anatomy.

Fig. 30. Periphery of central cylinder showing endodermoid layer with what appear to be bundles in early stage of development and radially arranged bundles. P2584 B bot #1 x 85.

Fig. 31. Detail of endodermoid layer and vascular bundles. P2584 B bot #10 x 200.

Fig. 32. Short tracheid from vascular plexus showing alternate pitting. P2584 B bot #13 x 330.

Fig. 33. Tracheid from vascular plexus showing pseudoperforation. P2584 B bot #13 x 400.

Fig. 34. Three adjacent tracheary elements showing cell arrangement that appears as a pseudoperforation in a different focal plane or when preservation is poor. P2584 B bot #13 x 400.

Fig. 35. Irregular tracheid from vascular plexus. P2584 B bot #13 x 330.

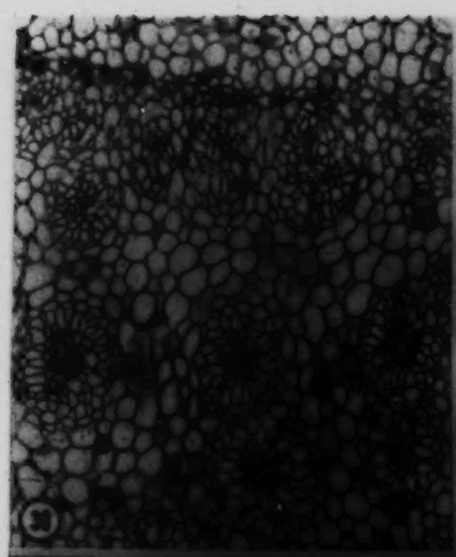
Fig. 36. Stem cross section showing vascular plexus. P2584 B bot #14 x 80.

Fig. 37. Thick-walled, pitted cells with dark contents. P2584 C top #3 x 200.

Fig. 38. Rhizome epidermis (ep) and cortex (co) without vascular bundles. Arrow marks outer limit of central cylinder (cc). P2584 C bot #36 x 100.

Fig. 39. Lignified ground tissue. P2584 C top #2 x 265.

Fig. 40. Septate fungal hyphae (arrows) in cortical cells of rhizome. P2584 B bot #10 x 290.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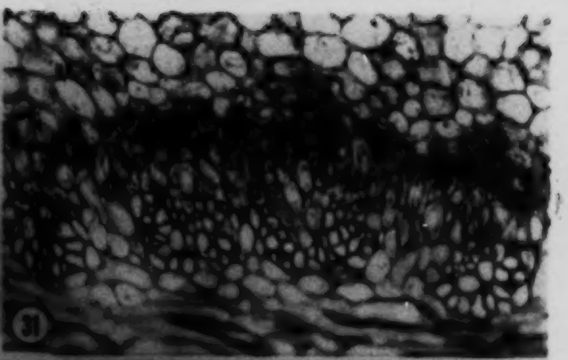
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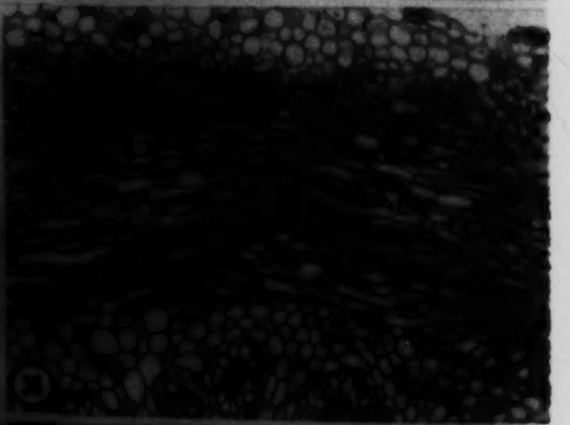
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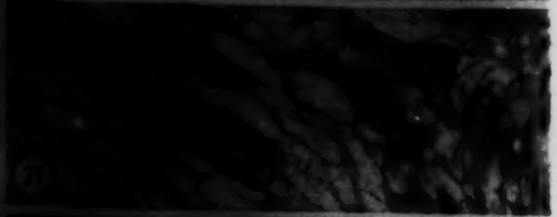
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Plate V, 5

Soleredera rhizomorpha gen. et sp. nov., root anatomy.

Fig. 41. Stem with attached roots and part of branch (arrow). P2584 B bot #1 x 8.

Fig. 42. Root steles at low magnification showing ring of spaces where phloem is not preserved that resembles a ring of vessels, large-celled epidermis (arrow) and underlying layer with small cells (arrowhead). P2584 B bot #1 x 27.5.

Fig. 43. Cross section of root showing stele, cortex (not preserved), epidermis (ep), exodermis (ex), and endodermis (en). Note U-shaped bands of xylem (xy) and thin-walled passage cells (arrows). P1243 C2 top #8 x 125.

Fig. 44. Root cross section showing thin-walled lignified ground tissue of pith, cortex, xylem (xy), phloem (ph), and fibrous ground tissue (f) surrounding the vascular tissues. P2584 B bot #14 x 177.

Fig. 45. Section of stele showing U-shaped thick-walled endodermal cells, phloem (ph), passage cells (pc), and one-layered pericycle (pc). P1243 D top #2 x 200.

Fig. 46. Longitudinal section showing scalariform-like wall thickenings on cells of endodermis. P1243 E top #6 x 415.

Fig. 47. Longitudinal section showing vessel member (vm) with oblique end walls and simple perforation plate visible at arrow. P2584 C bot #6 x 210.

Fig. 48. Face view of simple perforation plate (arrow) and alternate intervascular pitting. P2584 C top #2 x 300.

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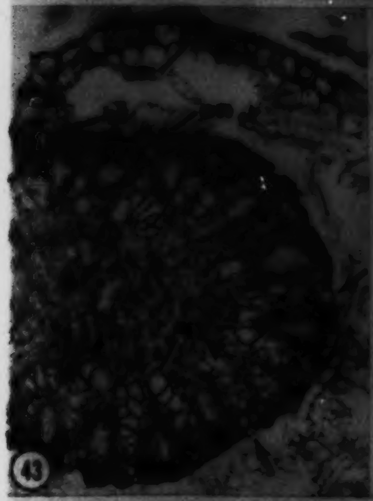
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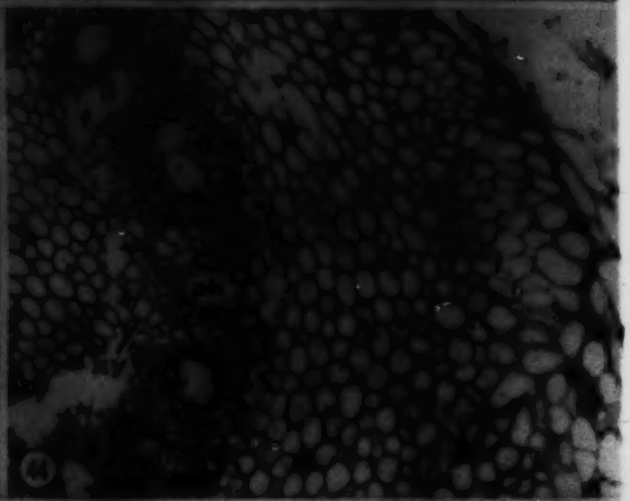
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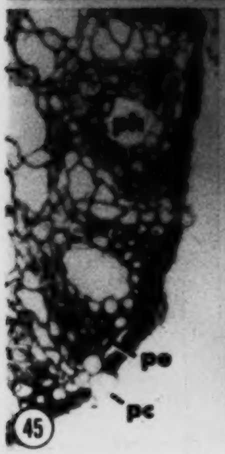

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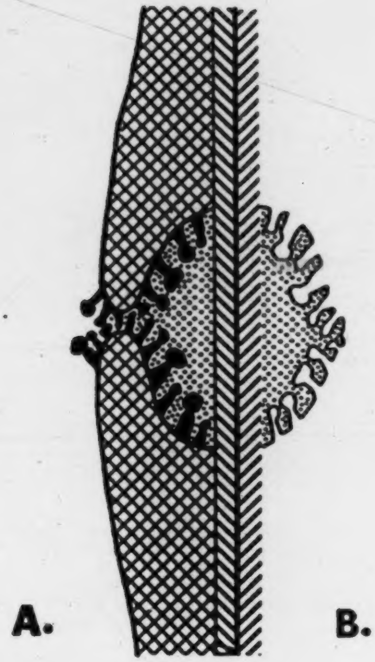
Plate V, 6

Fig. 49. Schematic drawing showing longitudinal section through bordered pit pair. A. Pit showing vestures attached to secondary wall (cross hatching) of the border, pit canal, and aperture. Stipples represent infilled pit cavity. B. Cast of pit cavity (stipples) with molds of vestures (white) left when secondary wall not preserved.



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Chapter 6: General Discussion

Paleobotanical studies have provided important information regarding the evolution of various extant taxa. The fossil histories of the Lycopsida (lycopods) and Sphenopsida (Equisetum) are two excellent examples for which there is an extensive fossil record documenting evolutionary changes that have taken place in these two classes since their first appearance in the early Paleozoic (Stewart, 1983). Owing to the fossil record we know that the herbaceous forms of these pteridophytes that comprise an insignificant part of our modern flora had, in the past, Permian and Carboniferous counterparts that were woody and tree-like (Stewart, 1983). Unlike today, these groups were among the most dominant plants at that time.

Recent studies of fossil angiosperms have begun to make significant contributions to our knowledge of the origin and evolutionary history of this plant group (Doyle, 1973, 1978; Hickey and Doyle, 1977; Thomas and Spicer, 1987). Prior to the 1960's, botanists presumed the fossil record to be of little significance in reconstructing angiosperm phylogeny (Delevoryas, 1968; Doyle, 1978; Thomas and Spicer, 1987). Most hypotheses concerning the origin and evolution of the angiosperms are based on comparative morphological studies of modern taxa (Huber, 1969; Doyle, 1973, 1978; Stebbins, 1974; Cronquist, 1988). These studies are important for documenting morphological, anatomical, and biochemical characters for use in angiosperm classification and phylogenetic analyses (e.g., Taylor and Hickey, 1990a, b). Many authors believe that the fossil record remains the only source of direct evidence on the early evolutionary history of this group (Doyle, 1973; Hickey and Doyle, 1977) and provides the strongest criterion on which to base character state polarities

(Crisci and Stuessy, 1980). Crisci and Stuessy (1980), however, also point out that since the fossil record is incomplete most systematists do not use fossil evidence.

Much uncertainty still surrounds the origin of angiosperms and their subsequent divergence into the two major groups that we recognize today: the dicotyledons and monocotyledons. Undisputed dicotyledon- and monocotyledon-like leaves and pollen occur contemporaneously in early Cretaceous sediments (Doyle, 1973; Hickey and Doyle, 1977). The consensus among botanists is that the monocotyledons are derived from the dicotyledons (Dahlgren and Rasmussen, 1983). However, Burger (1981) presents arguments to the contrary based on evidence from vegetative morphology, anatomy, and the fossil record. He suggests that the monocotyledons are the most primitive angiosperms and the dicotyledons have evolved from them.

Opinions vary as to which extant dicotyledonous group is most likely the sister group of the monocotyledons (Takhtajan, 1969, 1980; Huber, 1969; Stebbins, 1974; Thorne, 1976; Dahlgren and Rasmussen, 1983; Cronquist, 1988). The most persistent view envisions the monocotyledons as being derived from a primitive, herbaceous, aquatic stock of dicots resembling the modern Nymphaeales (Radford et. al., 1974; Burger, 1981; Cronquist, 1988). Similarities in habit, anatomy, and floral structure between the aquatic dicot order Nymphaeales and the monocot order Alismatales are usually cited as evidence for a close phylogenetic relationship between these two groups (Takhtajan, 1969, 1980; Cronquist, 1988). Some authors have suggested placing the Nymphaeales within the monocotyledons based on seedling structure (Haines and Lye, 1975). Still others have proposed assigning the monocotyledonous families Alismataceae, Limnocharitaceae, and Butomaceae to the Nymphaeales (El-Gazzar and Hamza, 1975).

The Alismatales have generally been regarded as a primitive order of monocotyledons that were derived from aquatic dicotyledons resembling most closely the Nymphaeales (Takhtajan, 1969, 1980; Cronquist, 1981, 1988). However, many of the similarities between the Nymphaeales and Alismatales are possibly convergences that have evolved in response to similar selective pressures related to growth in an aquatic habitat (Tomlinson, 1982). Recent evidence suggests characters traditionally considered primitive in some monocotyledons and their ancestors are probably specializations (Cheadle, 1953; Moore and Uhl, 1973; Tomlinson, 1982). For example, numerous stamens and carpels that are spirally-arranged have been considered to be the plesiomorphic character state in Alismatales. However, studies of flower development in this order suggests that the presence of numerous floral parts is a derived character state achieved through the secondary proliferation of simple trimerous flowers and there is no evidence of spiral arrangement (Singh and Sattler, 1972, 1977; Sattler and Singh, 1978). Butomaceae and Alismataceae possess vessel elements with simple perforation plates in the roots, also a specialized or derived character state in monocotyledons (Cheadle, 1953).

The fossil record of monocotyledons in general is poorly known. In a review of fossil monocotyledons, only about 20 of the nearly 100 monocot families are recognized as having a reliable fossil record (Daghlian, 1981). This low representation can be attributed to several factors. For example, in most extant floras dicotyledons are more abundant (Raven and

Axelrod, 1978; Tomlinson, 1980) with about 6 times as many dicot genera recognized as monocotyledonous genera (Daghlian, 1981). A similar bias appears among the angiosperms in fossil floras with relatively fewer monocotyledonous taxa present (Daghlian, 1981). The relatively higher abundance and diversity of dicotyledons in a particular fossil flora may be directly influenced by the type of depositional environment and taphonomic processes the plants of a particular flora undergo before becoming fossilized (Wilson, 1988a). Leaves, twigs, flowers, fruits, seeds, and pollen of woody, arborescent, deciduous dicotyledons are more likely to be carried by wind over greater distances to a site of deposition. Similar organs from smaller, herbaceous, non-deciduous monocotyledons would be less likely to reach the same site. Furthermore, woody tissues of dicotyledons are more resistant to decay and abrasion than the softer tissues that comprise the vegetative organs of most monocotyledons, thus increasing the probability that they will be preserved.

Many monocotyledonous remains, especially compressions of linear or strap-shaped leaves with parallel venation and various types of stems (e.g., rhizomes, bulbs, corms, culms), are difficult to assign to a specific family or higher taxonomic rank with any degree of confidence. Fossils of this type have been referred to the extant genera *Phragmites*, *Typha* and *Arundo* or the form genera *Cyperites* and *Arundites* (e.g., Hollick, 1936). These assignments suggest affinities with modern genera, but in most cases they should be considered dubious since venation patterns, internal anatomy, cuticle, and epidermal features have not been studied in detail. Numerous accounts of *Sparganium* (Sparganiaceae) fruits have been reported from Paleocene and younger deposits (Berry, 1924; Chandler, 1964; Hickey, 1977); however, the fossils assigned to this genus are suspect since they may be confused with *Platanus* infructescences.

TERTIARY ANATOMICALLY-PRESERVED MONOCOTYLEDONS

The Tertiary fossil history of monocotyledons is based primarily on disarticulated leaf compressions, molds and casts of fruits and seeds, and pollen (Daghlian, 1981; Muller, 1981; Collinson, 1983a, b, 1987; Schaarschmidt and Wilde, 1986). With the exception of silicified palm stems, anatomically-preserved monocotyledons are infrequently found in the fossil record (Tidwell and Parker, 1990), especially in sediments older than Oligocene.

In Europe, the Eocene London Clay flora has yielded pyritized molds and casts of fruits and seeds related to families such as Arecaceae, Araceae, and Cyperaceae (Reid and Chandler, 1933; Chandler, 1964; Collinson, 1983a, b). Silicified palm remains are abundant in the Deccan Intertrappean Series of India (Lakhanpal, 1970; Rao and Achuthan, 1971; Lakhanpal et al., 1979; Sheete and Kulkarni, 1980). Flowers, fruits, and vegetative remains of monocot families such as Sparganiaceae (Mahabale, 1953); Musaceae (Jain, 1963a, b); Cannaceae (Trivedi and Verma, 1971); Zingiberaceae (Sahni et al., 1934; Sahni, 1934), Cyclanthaceae (Trivedi and Verma, 1972); Pandanaceae (Nambudiri and Tidwell, 1978), and Pontederiaceae (*Eichornia*) (Patil and Singh, 1978) also have been reported. The Middle Eocene oil-shales at Messel, West Germany, are yielding abundant flowers, fruits, and seeds (Collinson, 1987). Monocot families recognized so far include Arecaceae, Cyperaceae, and

Cyclanthaceae (Schaarschmidt and Wilde, 1986; Collinson, 1987). Deposition in the oil-shales has allowed preservation of delicate, soft tissues, but unlike the Princeton chert fossils, specimens preserved in the oil-shale environment have undergone pronounced compression (Collinson, 1987).

In North America, there are scattered occurrences of silicified monocotyledonous remains, but all are found in deposits younger than Eocene. Remains of fruits, flowers, and seeds resembling Poaceae have been described from late Tertiary (Oligocene-Miocene) deposits of Nebraska (Thomasson, 1978, 1980, 1984, 1987) and the vegetative bodies of two fossil californian grasses, the upper Miocene, *Tomlinsonia thomassonii* (Tidwell and Nambudiri, 1989) and the Pliocene species, *T. stichkania* (Tidwell and Nambudiri, 1990). Just recently a *Yucca*-like monocotyledon (Agavaceae) has been described from Miocene deposits in Nevada (Tidwell and Parker, 1990).

Although *Equisetum*, ferns, conifers, and dicotyledons have been reported from the Eocene Clarno Formation (Arnold, 1944; 1952; Scott, 1954; Miller, 1973; Manchester, 1981), monocotyledons have yet to be described. At a site near the Princeton chert locality known as Vermillion Bluffs, G. M. Dawson (1879) noted "silicified grass stems" and other "vegetable fragments" that had weathered out of the sediments. However, Basinger (1981) recognized only *Eorhiza* rhizomes and *Metasequoia* cones at this locality. Very little is known about the internal structure of early Tertiary monocotyledonous vegetative and reproductive organs or the relevance this type of information might have to the systematic conclusions based on morphological features from compressed organs.

The Middle Eocene Princeton chert flora, however, has yielded a rich assemblage of anatomically well-preserved monocotyledonous vegetative remains. Exquisite cellular detail and three-dimensional preservation of the Princeton material has allowed the recognition of four distinct types of plants. Preservation of the most delicate tissues has provided a wide range of morphological and anatomical characters for comparing the fossils to extant taxa. However, despite exceptional preservation, several problems related to comparing, identifying, and classifying the Princeton monocots were encountered. A short discussion of some of the limitations and problems regarding both the nature of the fossil specimens and extant monocotyledons is presented.

LIMITATIONS IN THE STUDY OF PERMINERALIZED MONOCOTYLEDONS

Systematists working on living plants usually have abundant material at their disposal that represents all phases of the plant's life history. Angiosperm paleobotanists, on the other hand, usually have only fragmentary, disarticulated plant parts on which to base systematic conclusions since the preservation of in situ fossil plants showing attached organs in different life stages is rare. Most commonly, specimens are found as assemblages of dispersed vegetative and reproductive organs or fragments of these organs displaying various modes and qualities of preservation. This fragmentation may be a direct result of the plant's inherent growth and development (e.g., abscission of leaves, flowers, fruits) as well as disarticulation associated with the processes of death, decay, transportation, burial, and fossilization (Wilson, 1988a).

Paleobotanists in their descriptions of fossil remains are governed by the type and limited amount of taxonomic information obtainable from often fragmentary and poorly preserved isolated plant organs. Unfortunately, these organs are rarely flowers, but most commonly are compression/impressions of leaves, fruits, and seeds; molds and casts of fruits and seeds; and pollen. Individual fossil organs may closely resemble those of modern angiosperm taxa in morphology; however, the taxonomic and phylogenetic conclusions based on isolated organs alone, without the knowledge of the rest of the plant, can lead to a distorted view of the diversity and evolution of angiosperm taxa (e.g., Read and Hickey, 1972).

Paleobotanists investigating early angiosperms must work within a systematic framework based on studies of extant angiosperms. This poses several problems since angiosperm classifications are based largely on extant characters of flower, fruit, and seed morphology, plus additional information from vegetative morphology, anatomy, embryology, pollen, and cytology. Vegetative anatomical characters are less widely used and are seldom included in the diagnoses of extant angiosperms.

Studies regarding the systematic vegetative anatomy of monocotyledons (e.g., Solereder and Meyer, 1928, 1929, 1930; Metcalfe, 1960, 1971; Tomlinson, 1961, 1969, 1982; Cutler, 1969; Ayensu, 1972; Ambrose, 1980; French, 1984; Rudall, 1984, 1986; 1989; Tomlinson and Wilder, 1984; Wilder, 1984, 1985a-d, 1986a, b; Rudall et al., 1986) have provided descriptions and/or established characters of diagnostic importance at various taxonomic ranks within the monocots. However, the characters deemed taxonomically significant for living monocotyledons are based on sections of mature plant organs taken from a standard level (Tomlinson, 1961; Metcalfe 1971; Klotz, 1978). Unfortunately, it is difficult to know if sections of fossil organs directly correspond to those described for extant taxa. Also, structural features may change both qualitatively and quantitatively within a single organ from proximal to distal levels (e.g., Tomlinson, 1961; Rich, 1987; Waterhouse and Quinn, 1987) and result from differences in developmental stages of a particular organ.

Furthermore, descriptive studies of extant taxa often have been based on a limited number of genera and species. Consequently, the full range of character variability at the generic or specific rank is never fully established. Yet these characters are regarded as diagnostic for a particular taxon.

The structure of some characters, for example tracheary elements, can be difficult to interpret (Metcalfe, 1971). In monocots, the distinction between narrow vessels with long oblique scalariform perforation plates and tracheids with scalariform lateral wall pitting is not clear-cut especially when viewed at the light microscope level. This ambiguity has led to different interpretations of the same elements by different researchers (Wagner, 1977). Fahn (1954) has even proposed the term "vessel-tracheid" to describe tracheary elements in monocotyledons with vessel-like characteristics. Vessel-like tracheids have also been reported in the dicot genus Bubbia (Winteraceae) (Carlquist, 1983). Interpretation of tracheary elements in fossil plants is even more problematic since maceration techniques are not possible in many cases and identifications are based on serial longitudinal sections.

Plant organs can evolve at different rates and therefore fossil angiosperms may show structural features suggestive of affinities with a family based on that particular organ; however, if the rest of the plant were found, a closer relationship to another family might result.

Plants are very plastic and show a high incidence of homoplasy in response to their environment. Similar morphological and anatomical characters of vegetative and reproductive organs can occur in plants adapted to the same environmental conditions. For the paleobotanist this is problematic since similarities thought to reflect common ancestry may simply be parallel or convergent evolution of characters in totally unrelated taxa adaptated to a common habitat. Therefore, conclusive statements concerning phylogenetic relationships based on a limited number of vegetative characters should be avoided until as much information about a particular fossil plant is known.

VEGETATIVE CHARACTER STATES IN THE PRINCETON MONOCOTYLEDONS

The Princeton monocotyledons show both unspecialized (primitive) and specialized (derived) vegetative characters for the monocotyledons as a whole and at their respective lower taxonomic ranks. A survey of character states in monocotyledons and their systematic distribution throughout the group has been presented by Dahlgren and Clifford (1982). An estimation of the relative temporal sequence or polarity of selected characters from among those described by Dahlgren and Clifford (1982) has been provided by Dahlgren and Rasmussen (1983). Polarities for these characters were determined using a set of monocotyledon-like dicotyledons (i.e., Magnoliidae) as the functional out-group (Dahlgren and Rasmussen, 1983). Several of the vegetative characters evaluated by Dahlgren and Rasmussen (1983) are applicable for discussion here. Among these are plant habit, degree of vessel specialization, vessel distribution in the plant, leaf morphology, venation, laticifers, and silica bodies. Also, Uhl and Dransfield (1987) have listed several evolutionary trends in palms. In addition to these characters, CHEADLE and UHL (1948) have described 6 types of vascular bundles (i.e., I, II, IIIa, IIIb, IV, V) in monocotyledons and discussed their putative evolutionary development.

Plant Habit

For angiosperms as a whole, an arborescent or shrubby, woody habit has been considered to be plesiomorphous and a small herbaceous habit (e.g., rhizomes, tubers, bulbs, non-woody dicots) apomorphous (Radford et al., 1974; Stebbins, 1974; Cronquist, 1988). The basis for this presumed polarity is partly founded in the currently accepted hypothesis that envisions the proto-angiosperm as a tree or shrub with flowers of moderate size, numerous parts, and conduplicate carpels (Taylor and Hickey, 1990a, b). However, based on a character and phylogenetic analysis, Taylor and Hickey (1990a) and others (Dahlgren et al., 1985) suggest that the ancestral angiosperm was a small, rhizomatous or liana-like perennial that lacked vessels, and had small flowers with few parts.

With respect to monocotyledons, Meeuse (1975) regards two growth habits as primitive. The first type is characterized by plants with rather large, unbranched, prostrate or ascending aerial stems, whereas plants with a subterranean, rhizomatous system with simple or more complex branching represents the other. In Zingiberales, Tomlinson (1962, 1969) considered the tree habit to be the plesiomorphic character state for the order based on the occurrence of arborescent stems in the Strelitziaceae, a primitive family with respect to reproductive characters. In contrast, Dahlgren and Rasmussen (1983) consider the presence of sympodially-branched rhizomes to be plesiomorphic for the order. However, for monocotyledons as a whole, Moore and Uhl (1973) caution against designating arborescence or herbaceousness as primitive as this can lead to inconsistent correlations of other unspecialized character states.

The three Princeton monocotyledons: Soleredera (Liliales), Uhlia (Palmae), and Ethela (Cyperaceae/Juncaceae) have rhizomatous stems. The presence of rhizomes can be interpreted to be either the plesiomorphic character state in those families in which bulbs occur or as an apomorphic reversal in families where bulbs dominate (Dahlgren and Rasmussen, 1983).

Soleredera rhizomorpha

Based on available reports of vegetative anatomy of the Liliales, Soleredera closely resembles the Agavaceae, Iridaceae, and Liliaceae in certain aspects of plant habit, bundle morphology in cross section, ground tissue, and specialization and organographic distribution of vessels. In a phylogenetic analysis of the Liliales-Orchidales complex, Dahlgren and Rasmussen (1983) considered the presence of rhizomes to be the plesiomorphic character state for this clade. Liliales as defined by Dahlgren and Rasmussen (1983) include among others, the Liliaceae *sensu stricto* and Iridaceae. Soleredera shows a close resemblance to these families as well as others in the order. Therefore, within the Liliales, the rhizomatous habit of Soleredera displays the less specialized (primitive) character state.

Uhlia allenbyensis

Evolutionary trends for several characters related to the growth habit and stems of palms have been suggested based on comparative studies of extant palms (Moore, 1973; Moore and Uhl, 1982; Uhl and Dransfield, 1987). Dahlgren and Rasmussen (1983) consider the arborescent habit to be a synapomorphy for the Areciflorae (=Arecales, Pandanales, Cyclanthales). However, the Areciflorae may not be monophyletic (Dahlgren and Rasmussen, 1983; Tomlinson and Wilder, 1984; Uhl and Dransfield, 1987) but the features shared by these groups are not patristic (Tomlinson and Wilder, 1984). Considering arborescence as a synapomorphy in defining the Areciflorae as a clade at this time seems questionable. If for example, the Areciflorae are monophyletic and the arborescent habit in palms is primitive, as suggested by Tomlinson (1970), then the arborescent habit at the level of the Areciflorae could be a symplesiomorphy rather than a synapomorphy.

Uhl and Dransfield (1987) refer to the palm habit as being either solitary (i.e., monopodial) or clustering (i.e., sympodial). According to Uhl and Dransfield (1987) a solitary or monopodial habit is considered to be derived from a clustering or sympodial habit. The state of this character in Uhlia is unclear. All the specimens of Uhlia are single stems. Therefore, one might conclude that Uhlia had a solitary habit as found, for example, in Brahea decumbens. However, the clustering habit cannot be totally ruled out since it is possible that each specimen represents the main shoot or a lateral branch. Stems of clustering palms grow by producing new shoots from axillary buds located near the base of each shoot (Uhl and Dransfield, 1987). As mentioned previously, peripheral traces in the stem of Uhlia may represent traces to axillary branches, but it is unclear whether these are near the stem base. If so, then Uhlia would have a growth habit similar to Serenoa repens.

Also in palms, shoot size has gone from being moderate to large or from moderate to small. Based on comparisons to extant palms, Uhlia could be considered moderately-sized. However, specimens of Uhlia are incomplete radially and the plants may have been juvenile (Tomlinson, personal communication).

Ethela sargantiana

Stems of Ethela are also rhizomatous, small, and herbaceous. Based on features of leaf anatomy, Ethela most closely resembles the families Cyperaceae and Juncaceae. Within Liliopsida these families are considered to be among the most derived angiosperm groups (Cronquist, 1988). Despite the antiquity of Ethela, this plant shows anatomical and morphological features comparable to extant taxa in these families.

Vessel specialization, organographic distribution, and vascular bundle organization

The types of vessels and their distribution among plant orders provide important characters for estimating evolutionary sequence and the degree of advancement in monocotyledons (Dahlgren and Rasmussen, 1983). Our current understanding of xylem evolution in monocotyledons is based primarily on comparative studies of extant monocot taxa by Cheadle (1942, 1943, 1944, 1953). Cheadle proposed that vessels originated from tracheids and evolved throughout the plant body in the following order: appearing first in the late metaxylem of the roots, subsequently in the stems, inflorescence axes, and ultimately in the leaves. Paralleling this phylogenetic progression in the plant was a concurrent shift from the least specialized (primitive) type of vessel with long oblique scalariform perforation plates with numerous bars to the most specialized (derived) state, vessels with transverse end walls and simple perforations (Cheadle, 1953).

Polarization of vessel character states in monocotyledons has been discussed by Cheadle (1953) and Dahlgren and Rasmussen (1983). Cheadle (1953) considered the presence of tracheids or lack of vessels in the organs of monocotyledons to represent the least specialized (primitive) character state. Based on xylem evolution, Cheadle (1953) considered that the monocotyledons most likely evolved from extinct or living vesselless, woody dicotyledons rather than from aquatic, vesselless, herbaceous dicotyledons such as the Nymphaeales.

Vessels are lacking in the majority of taxa in the Nymphaeales (except Nelumbo; Kosakai et al., 1970) and Alismatidae (Tomlinson, 1982). This absence has been used as evidence to support a lack of vessels as the plesiomorphic character state in monocotyledons (Cronquist, 1988). However, recent evidence suggests an alternative view that regards the aquatic Alismatidae and Nymphaeales as being secondarily specialized (derived) (Huber, 1969; Tomlinson, 1982; Dahlgren and Rasmussen, 1983). Based on this premise, the ancestral monocotyledons could have possessed vessels with scalariform perforation plates in their roots and stems, but these were eventually lost in response to adaptation to an aquatic habitat. Lack of vessels in roots and stems therefore could be considered an apomorphic character state within certain groups of monocotyledons (Dahlgren and Rasmussen, 1983).

Soleredera rhizomorpha

Roots of Soleredera have vessels with simple perforation plates, whereas vessels are absent in the rhizomes and aerial stems. These character states are found in many extant families of the Liliales *sensu lato* (Dahlgren and Clifford 1982). Dahlgren and Rasmussen (1983) consider the vesselless condition in stems and roots of the Liliidae to be an apomorphy. If the characters are polarized in this way, lack of vessels in the rhizomes and aerial stems of Soleredera would represent the apomorphic character state. However, it is just as plausible, following Cheadle's (1943) view of xylem evolution, to consider the vesselless condition in the rhizomes and aerial stems of Soleredera to be plesiomorphic. The presence of simple perforation plates in the root vessels of Soleredera represents a more specialized (derived) character state.

Soleredera displays a specialized (derived) vascular bundle organization. Collateral bundles in Soleredera correspond to Cheadle and Uhl's (1948) Type II, whereas the amphivasal bundles in Soleredera represent Type V. Type II bundles are characterized by a V-shaped xylem strand composed primarily of tracheids (Cheadle and Uhl, 1948). Among the groups of monocotyledons examined by Cheadle and Uhl, Type II bundles were found to be relatively uncommon. From a phylogenetic point of view, Type II bundles were considered to be derived from the least specialized (primitive) Type I bundles. Type V bundles, on the other hand probably arose separately from any of the remaining five types (Cheadle and Uhl, 1948).

Uhlia allenbyensis

Vessels occur in both the stems and roots of the Princeton palm, *Uhlia allenbyensis*. The vessels in both these organs show simple perforation plates. Simple perforation plates represent a more specialized (derived) character state. However, in the stem a few vessels show a transitional stage with short, scalariform perforation plates consisting of only 2-4 bars. The significance of this character state is uncertain. In terms of xylem evolution, the presence of a few vessels with scalariform perforation plates can be explained as an intermediate stage in the evolution toward a stem with all vessel elements having simple perforations. It is interesting to note that vessels with these two types of perforation plates have been reported in rhizomes of the extant palms, *Serenoa repens* and *Rhapidophyllum hystrix* (Tomlinson, 1961). This suggests that the level of specialization of tracheary elements in *Uhlia* is comparable to that found in rhizomatous palm genera growing today, nearly 50 million years later.

Ethela sargantiana

Vessels have been identified in both roots and leaves of *Ethela*. According to Cheadle (1953), the presence of vessels in leaves suggests their co-occurrence in the stems. Therefore, the rhizomes of *Ethela* may have vessels even though the tracheary elements in these organs have not been positively identified as vessels. Nonetheless, in *Ethela* vessels of the roots and leaves have scalariform perforation plates. In the roots, perforation plates are relatively short with up to about 12 bars. Vessels in the leaves, however, have numerous bars (ca. 40-50) on very oblique end walls. The presence of scalariform perforation plates in the vessels of the roots and stems represent a less specialized character state with respect to xylem evolution in monocotyledons as a whole and for the families Cyperaceae and Juncaceae. Presence of vessels in the leaves of _Ethela_ documents the appearance of vessels in this organ at least by the Middle Eocene for plants with commelinalean affinities.

Heleophyton helobioides

With respect to bundle morphology, _Heleophyton_ has Type I bundles (Cheadle and Uhl, 1948). Type I bundles have been considered to be the most primitive and that type from which all others have evolved (Cheadle and Uhl, 1948). Type I bundles occur in both the Nymphaeales (_Nymphaea_) and Alismatales (Butomaceae). In light of the current findings relative to the specialization of these two orders, conferring primitiveness to this bundle type seems questionable since this bundle structure may actually represent a more specialized organization that has evolved in response to selective pressures imposed by an aquatic habitat. The presence of Type I bundles in _Heleophyton_ establishes the evolution of this bundle type by the Middle Eocene.

Leaf morphology and venation

Heleophyton helobioides

Heleophyton, _Uhlia_, and _Ethela_, all show leaf remnants. Although _Heleophyton_ is represented only by a fragment of a small petiole, one can infer from its morphology and anatomy, the petiolate nature of at least some leaves of _Heleophyton_. It should be noted here that due to the aquatic nature of _Heleophyton_ and its relationship to Alismataceae, individual plants are capable of producing both floating or emergent petiolate, reticulate-veined leaves or submerged linear, non-petiolate, parallel-veined leaves on the same plant (Magee, 1957; Cronquist, 1988). Leaves of Heleophyton may have had a sheathing base and a broad distal lamina with reticulate venation similar to leaves found in extant Alismataceae.

Within the Alismatales, a petiolate, net-veined leaf type is considered by Dahlgren and Rasmussen (1983) to be plesiomorphic, whereas the linear, parallel-veined leaves of Butomaceae are apomorphic. In contrast, based on earlier work by de Candolle (1827) and Arber (1918, 1925), Cronquist (1988) suggests that the petiolate leaves of the Alismatales are secondarily derived by expansion of the petiole tip. The lamina in this case is not strictly homologous to the leaf blade of dicotyledons. However, based on developmental studies of monocotyledonous leaves, Kaplan (1973) found the petiole tip or upper leaf zone to be the positional homolog of a dicotyledonous leaf. He also suggests that the unifacial or linear leaves may actually represent derived forms that have evolved in response to extremely dry or wet environments. Therefore, depending on which criteria and level of comparison one uses to polarize the character states of leaf form and venation, the petiolate leaves of Heleophyton show the plesiomorphic state at the level of the angiosperms. However, within the monocotyledons, this leaf type can be considered either plesiomorphic (Dahlgren and Rasmussen, 1983) or apomorphic (Cronquist, 1988).

Ethela sargantiana

Leaves of Ethela have broad sheathing leaf bases with a single row of alternating major and minor veins. Transverse veins have not been observed. From these features leaves of Ethela most likely were parallel-veined and non-petiolate. The distal portions of attached leaves are incomplete and so the morphology of the entire leaf of Ethela is wanting. However, isolated leaf segments are dorsiventral with a single row of veins all oriented with their xylem directed toward the adaxial surface. This suggests Ethela had leaves that were dorsiventrally-flattened rather than linear and unifacial or ensiform. Within monocotyledons, parallel-veined non-petiolate leaves are considered to be plesiomorphic.

Ethela combines features of the Cyperaceae and Juncaceae. Silica bodies are present in cyperaceous leaves, but are absent in the leaves of Juncaceae. Silica bodies have not been found in leaves of Ethela. Presence of silica bodies in several different groups of monocots indicates these structures have arisen independently as apomorphies (Dahlgren and Rasmussen, 1983). Lack of silica bodies in Ethela is therefore plesiomorphic.

Uhlia allenbyensis

Palm leaves show several evolutionary trends in morphology and anatomy (Moore and Uhl, 1982; Uhl and Dransfield, 1987). The leaf blade ranges in form from palmate, costapalmate, pinnately-ribbed, to pinnate. The evolution of the different types of palm leaves still remains unresolved. It has been suggested that all leaf types are derived from leaves resembling the simple, undivided eophyll of coryphoid and other palms (Uhl and Dransfield, 1987). Although the fossil record is incomplete, the first recognizable fossil palm leaves are costapalmate (Berry, 1911) and occur in the Upper Cretaceous (Santonian or Coniacian) Magothy Formation

(Christopher, 1979). Pinnate leaves appear somewhat later in the Maastrichtian, while palmate leaves are found in the Paleocene (Daghlian, 1981). Based on fossil evidence one might conclude that the costapalmate leaf represents the least specialized type; however, the fossil record is incomplete.

Palms had already undergone a rapid diversification by the Middle Eocene inhabiting numerous regions throughout the world (Uhl and Dransfield, 1987) and with all leaf types evolved by that time (Read and Hickey, 1972; Daghlian, 1981). Midrib structure in Uhlia corresponds to that found in induplicate palm leaves. With the exception of Phoenix, only costapalmate and palmate leaves are induplicate. Although the costapalmate or palmate nature of Uhlia is not yet known, Uhlia shows a more derived leaf morphology.

Certain anatomical characters of palm vegetative organs are considered to be of diagnostic significance in distinguishing palms at various taxonomic levels (Tomlinson, 1961; Moore, 1973; Klotz, 1977, 1978). The most important characters in petioles are the number of wide metaxylem vessels and phloem strands in the central vascular bundles (Parthasarathy, 1968; Moore, 1973; Klotz, 1977, 1978; Moore and Uhl, 1982; Uhl and Dransfield, 1987). Interpreting these characters in Uhlia is somewhat difficult since the majority of specimens are either remnants of attached petiole bases or isolated fragments of only the peripheral regions of the petioles. In these specimens, bundles farthest from the edge of the petiole fragment were used in determining the state of this character. The most complete specimens show that the bundles have mostly one wide metaxylem vessel. Occasionally bundles with two or more vessels were observed; however, as pointed out by Klotz (1978), discrepancy in vessel numbers may result if sections are taken from different levels. For example, vascular bundles in sections taken from just below the insertion of the lamina or lowest leaflets may show more numerous vessels due to branching of the tracheary elements related to lamina or pinna trace formation (Klotz, 1978). Single vessels may appear as two if sectioned at the level of the perforation plate (Klotz, 1978).

Vessel number is relatively constant in certain major groups of palms (e.g., lepidocaryoid), but variable in others (e.g., coryphoid). Therefore, use of this character in combination with others for taxonomic purposes at the generic rank seems warranted, but its application in cladistic analysis needs further investigation, particularly with respect to the influence developmental aspects might have on vessel number.

Taxonomic and phylogenetic significance has been given to the number of phloem strands in the petioles of palms, but the usefulness of this character seems dependent on the development of the fibrous partitions in these bundles. Studies on the development of palm leaves have dealt primarily with the gross morphological aspects of these organs rather than their internal structural development. Petioles in which the vascular bundles have two phloem strands are borne by stems that have vascular bundles with a single phloem strand. Determination of phloem strand number in extant palms is based on sections from mature petioles taken from a standard level usually about midway between the base and insertion of the lamina (Klotz, 1977). Documenting the course of development of the fibrous partitions in petiole bundles and the range of variation in this character from the leaf base through more distal sections undoubtedly would increase the usefulness and significance of this character in the taxonomy of both extant and fossil palms.

The number of phloem strands in the central vascular bundles of palm petioles varies from one (e.g., tribe Borasseae), two (e.g., some Corypheae), or three (e.g., Sabal) (Tomlinson, 1961; Parthsarathy, 1968; Klotz, 1977). Phloem strand number results from the dissection of the phloem by the development of fibrous partitions. Bundles with one strand lack fibrous partitions while those with two strands have a median partition. In most palms, phloem strand number appears to be a constant feature at the generic rank with genera showing either one or two strands. However, in a study of the metaphloem in palm vegetative organs, Parthasarathy (1968) noted that phloem strand number in some genera was difficult to determine and therefore these genera could not be classified as having one or two strands.

Much emphasis has been given to the taxonomic and phylogenetic significance regarding the number of phloem strands in the central vascular bundles of palm petioles (Tomlinson, 1961; Moore, 1973; Moore and Uhl, 1982; Uhl and Dransfield, 1987). According to Uhl and Dransfield (1987), central vascular bundles with a single phloem strand are considered to be plesiomorphic, whereas bundles with two strands are apomorphic. However, the variability of this character in Uhlia and some extant palms raise questions about the polarization and usefulness of this character in phylogenetic analyses. More realistically three character states probably occur among fossil and extant palms. One phloem strand, two strands, or both may occur in one taxon.

Laticifers

Of the Princeton monocot taxa described, only *Heleophyton* has affinities with an extant family, the Alismataceae, in which most genera have laticifers. Laticifers have not been identified in *Heleophyton*. According to Dahlgren and Rasmussen (1983), the presence of laticifers is a form of specialization and therefore an apomorphic character state. Laticifers occur in many different groups of monocotyledons and therefore are polyphyletic (Dahlgren and Rasmussen, 1983). If *Heleophyton* does lack laticifers this could be considered a plesiomorphic condition.

Silica bodies

Ethela sargantiana

In Cyperaceae, silica bodies are found in the epidermal cells of the leaves of most genera, whereas these structures are absent in the Juncaceae. Dahlgren and Rasmussen (1983) consider presence of silica bodies as an apomorphy that has arisen independently in a number of monocotyledonous orders. Their absence in Juncaceae is considered the plesiomorphic state. On the other hand, silica bodies occur in the majority of taxa in the Cyperaceae and is the most common character state. If one employs the commonality principle (Crisci and Stuessy, 1980), presence of silica bodies could be considered the plesiomorphic state within the Cyperaceae, rather than the derived state. Taylor and Hickey (1990b) have suggested that the ancestral angiosperm possessed silica bodies throughout the entire plant body. Silica bodies are interpreted to be absent in *Ethela*. Lack of silica bodies in *Ethela* would be considered the plesiomorphic state based on Dahlgren and Clifford's (1982) polarization of this character.

Uhlia allenbyensis

Silica bodies of a different type than those in the Cyperaceae occur in the Palmae. Silica bodies in palms are found associated with the peripheral fibers of the vascular bundles and small fibrous strands in the stems, petioles, and laminae (Tomlinson, 1961). Silica bodies are ubiquitous in the palms and are either hat-shaped or spherical and druse-like (Tomlinson, 1961). The commonality of this character suggests presence of silica bodies is the plesiomorphic character state within palms. Silica bodies are present in Uhlia.

ENVIRONMENTAL INFERENCES

Several interpretations regarding the paleoenvironment of the Princeton chert locality have been suggested. Boneham (1968) considered the site to most likely represent a swamp or acid bog. Basinger (1976a, 1981) envisioned the Princeton locality as a marsh-like area that was periodically flooded or inundated by silica rich water from local geysers. More recently, evidence from plant and animal remains has been used to interpret the chert as deposition in a quiet lake or pond (Erwin and Stockey, 1989; Cevallos-Ferriz and Stockey, 1990b). Thin ash layers interbedded with the chert and coal layers have been identified in the section suggesting the source of silica could have been from ash produced by periodic volcanic eruptions (Stockey, pers. comm.).

The types of wetlands mentioned above are classified based on the amount and permanence of water and the dominant vegetation in the area (Mason, 1957; Magee, 1981). Swamps are either seasonally saturated with water to the surface or permanently flooded. The dominant vegetation consists of trees and shrubs, but not to the total exclusion of herbaceous plants (Mason, 1957; Magee, 1981). Most of the Princeton chert plant remains include fragments of dicot wood, roots, leaves, twigs, flowers, fruits, and seeds, plus the wood, roots, leaves, and cones of Metasequoia and Pinus. These remains indicate the presence of a diversity of dicot and coniferous trees, a floristic feature consistent with a swampy environment (Godfrey and Wooten, 1979; Magee, 1981). However, the systematic affinities of most of the remains described so far are not swamp dwelling taxa, but probably inhabited drier sites in an adjacent community (Miller, 1973; Stockey, 1984; Cevallos-Ferriz and Stockey, 1990a). Also, many of these remains are small and uncommon. Large pieces of wood or evidence of rooted tree stumps in the chert are very rare perhaps suggesting a habitat other than a swamp. The largest plant fragments found so far are the rooted, in situ rhizomatous stems of Uhlia that measure up to 9 cm wide.

Bogs are characterized by floating mats of vegetation located along shorelines of a lake or pond; such mats grow outward from the shore over the water surface (Magee, 1981). The principal component of such mats is often Sphagnum moss which supports smaller, herbaceous plants on its surface. Remnants of a moss gametophyte have been found in the chert (Basinger and Rothwell, 1977), but no extensive bryophytic remains have been identified to date that might be suggestive of a mat-type vegetation. If bryophytic remains had been present, it most likely would have been well-preserved along with the other chert plants (Knoll, 1985).

Marshes are typically covered seasonally or permanently by about six inches of water (Magee, 1981). Dominant marsh plants are typically herbaceous, emergent monocotyledons such as *Sagittaria* (Alismataceae), *Typha* (Typhaceae), and *Pontederia* (Pontederiaceae) (Mason, 1957; Magee, 1981). The presence and/or abundance of the monocotyledons *Heleophyton* (Alismataceae), *Uhlia* (Palmae), *Ethela* (Cyperaceae/Juncaceae), and *Keratosperma* (Araceae) in the chert provides support for a marshy environment.

Lakes or ponds are characterized by a conspicuous open water surface that is permanent or at a fairly fixed level (Mason, 1957). Lakes can merge with marshes to form "marshy lakes" (Mason, 1957; Godfrey and Wooten, 1979). As mentioned previously, recent evidence based on plant and animal remains suggests the Princeton chert site may represent a quiet lake or pond (Stockey, 1987; Erwin and Stockey, 1989; Cevallos-Ferriz and Stockey, 1990b). Fish bones have not been identified in the chert, but bones of the freshwater fishes *Amia* and *Libotonius* and isolated remains of small suckers, genus *Amyzon*, do occur in a layer of black shale above the chert (Wilson, 1980, 1982). Found associated with the fish are bones of a trionychid turtle (Wilson, 1982). Also, other turtle bones of unknown affinity have been found in the chert. Identification of these bones will add valuable information for reconstructing the paleoenvironment at Princeton.

The monocotyledonous remains in conjunction with the aquatic/semiaquatic dicots described so far in the chert provide strong support for interpreting the Princeton site as a lake or pond with marsh-like areas developed in shallower waters along the lake margin. Of particular significance is the presence of abundant seeds of Nymphaeaceae, *Allenbya collinsonae* Cevallos-Ferriz and Stockey (1989), araceous seeds described as *Keratosperma* (Cevallos-Ferriz and Stockey, 1988), and rhizomes of the semiaquatic, monocot-like dicotyledon, *Eorhiza arnoldii* (*Incertae sedis*) (Robison and Person, 1973; Stockey and Cevallos-Ferriz, 1987).

As mentioned previously, marshes are inhabited primarily by emergent monocotyledons such as *Sagittaria* (Alismataceae), *Typha* (Typhaceae), and sedges (Cyperaceae) (Mason, 1957; Magee, 1981). *Typha* is often the most dominant plant forming dense stands in shallow water from extensive, stout rhizomes. *Typha* has a good fossil record dating back to the Paleocene (Daghlian, 1981). *Typha* megafossils are found in Eocene to Oligocene sediments in North America (Daghlian, 1981). *Typha* has not been identified in the chert, but the presence of numerous rhizomes of *Eorhiza* suggests that this plant could have filled a similar ecological niche as *Typha* does today. The monocot-like vegetative body of *Eorhiza* (Stockey and Cevallos-Ferriz, 1987) could be considered to be analogous to that of *Typha*. *Eorhiza* is sufficiently similar to that of *Typha* that if *Eorhiza* were found in a compressed state, it might easily be identified as a monocotyledon.

Structural features in *Heleophyton* such as bundles with a reduced xylem strand, thin-walled tracheary elements, a well-developed phloem strand, a protoxylem lacuna surrounded by thin-walled cells with thickened inner walls next to the lacuna, and aerenchymatous ground tissue are adaptations to an aquatic or semiaquatic habitat. Also, shape and internal structure of *Heleophyton* plus its systematic affinities suggest that at least some leaves of *Heleophyton* were probably petiolate with a sheathing base and a broad expanded blade similar to that found in the alismatacean genera *Sagittaria* and *Echinodorus*. *Heleophyton* probably grew rooted in shallow water around the lake margin with leaf blades fully emergent or floating and in association with Eorhiza, Ethela (Cyperaceae/Juncaceae), Allenbya, and Keratosperma.

Uhlia has aerenchymatous ground tissue in the petioles, stems, and roots, but the presence of simple perforation plates in the roots and stems suggests that these plants probably occupied drier sites near the lake margins, possibly as part of the understory vegetation. The presence of Uhlia in the Princeton chert is significant in that it implies a subtropical to tropical climate that was warmer and/or wetter in this region during the Middle Eocene than it is today. Further evidence for a warm climate is reflected in the thick adaxial cuticle, stomata restricted to the abaxial surface, and a differentiated palisade in the laminae. A warm and humid climate (i.e. mean annual temperature of 20°, annual temperature range of 12°, and annual percipitation of 200 cm) for this region during the Eocene also has been suggested based on pollen analysis (Rouse and Mathews, 1979; Mathews and Rouse, 1984; Wilson, 1988b). It is interesting to note that Uhlia belongs to the coryphoid palms, a group that contains some of the most primitive members in the family (Uhl and Dransfield, 1987) and includes those palms which are the most cold tolerant (van der Burgh, 1984). Both Rhapidophyllum and Serenoa are found in moist or wet sites in the southeastern U.S.A. (Shuey and Wunderlin, 1977) whereas species of Brahea occur on limestone slopes and other outcrops in dry areas in the southwestern U.S.A. and Mexico (Uhl and Dransfield, 1987).

Soleredera (Liliales), on the other hand, shows no anatomical features to indicate that it was growing in water. Rather, Soleredera possesses features more indicative of a drier site, such as root vessels with simple perforations and lack of aerenchymatous ground tissue. However, Soleredera is represented by rhizomes with numerous adventitous roots that suggests it may have been preserved in growth position or transported only a short distance prior to being fossilized. Therefore, Soleredera may have inhabited drier sites at the very edge of the lake. These drier areas might have resulted from a lowering of the water level in the lake.

CONCLUSIONS

Anatomically-preserved monocotyledons are rare in the fossil record. The present study has shown that the Middle Eocene Princeton chert locality is significant in having yielded the oldest and most diverse assemblage of exquisitely-preserved monocotyledonous remains in North America. Fossil records for four of the five subclasses of monocotyledons are represented in the chert. These include Alismatidae (Heleophyton helobioides), Arecidae (Uhlia allenbyensis), Commelinidae (Ethela sargantiana), and Liliidae (Soleredera rhizomorpha).

Discovery of the small petiole described here as Heleophyton helobioides represents the first anatomically preserved vegetative megafossil with alismatacean affinities to be reported from North America. Prior to Heleophyton, bona fide megafossil remains of the Alismataceae were known only from Oligocene and younger deposits (Daghlian, 1981). Presence of Heleophyton in the Middle Eocene supports Daghlian's (1981) suggestion that the Alismataceae had evolved prior to its appearance in the Oligocene, possibly in the Paleocene.

Abundance and exquisite preservation of the Princeton chert remains has made it possible to reconstruct the vegetative bodies of two monocotyledons from the material examined in this study. The first is a rhizomatous palm described here as Uhlia allenbyensis Erwin and Stockey. Based on midrib structure and the presence of 1-2 phloem strands in the vascular bundles of the petioles, Uhlia most closely resembles the coryphoid palms. The presence of fibrous strands in the central ground tissue of the stems suggests a closer relationship to the coryphoid genera Rhapidophyllum and Brahea. However, midrib and petiole anatomy is most similar to Brahea and its close relative Serenoa. Internal structure of the laminae on the other hand more closely resembles Rhapidophyllum. Although Uhlia shows phenetic similarities to these coryphoid genera, additional specimens showing actual organic attachment between the petioles, midribs, laminae, and especially the reproductive organs is needed before definitive conclusions concerning the phylogenetic relationship of Uhlia can be made. Also, additional information is needed to document the variability with respect to ecological factors and development in order to fully establish the diagnostic value of extant palm vegetative characters.

Cyperaceous remains are common in Eocene deposits throughout the world (Daghlian, 1981; Collinson, 1987); however, most of the fossil record for this family is based on morphological evidence from molds and casts of fruits and seeds (Daghlian, 1981; Collinson 1983a, 1987; Friis, 1985). The fossil record of Juncaceae however, is comparatively very poor (Daghlian, 1981; Friis, 1985). The small herbaceous plant described here as Ethela sargantiana Erwin and Stockey is significant in that it combines anatomical features of both families. Leaves of Ethela are most similar to Cyperaceae in sclerenchyma shape and distribution; however, *Ethela* has narrow lateral vessels in the veins of the leaf, a feature more common to Juncaceae, whereas two wide vessels typically are found in the bundles of cyperaceaous leaves. Silica bodies in the epidermal cells above the sclerenchyma strands is also a characteristic feature of Cyperaceae (Metcalfe, 1971); however, silica bodies have not been observed in *Ethela* and are interpreted as being absent. In this feature, *Ethela* closely resembles the Juncaceae (Cutler, 1969; Metcalfe, 1971).

Cyperaceae and Juncaceae are considered to be closely related and separable on only a few reproductive characters (Dahlgren and Clifford, 1982). *Ethela* possesses no distinctive features for assignment to either the Cyperaceae or Juncaceae, although certain anatomical characters suggest affinities with these two families. Once the reproductive organs of this plant are known a more refined taxonomic treatment of *Ethela* will be possible.

Soleredera *rhizomorpha* represents the oldest report of permineralized megafossil remains with lilialean affinities from North America. Presence of vestured pits in vessels of *Soleredera* is the first report of these structures in monocotyledons. This finding may warrant future study of extant monocot vessels with respect to this feature. The stems of both *Soleredera* and *Uhlia* show potential for cinematographic analysis of the vascular system in order to compare the fossil systems with those known for extant monocots (Zimmermann and Tomlinson, 1965, 1971, 1974, Tomlinson, 1984). Zimmermann and Tomlinson (1974) have suggested the potential use of vascular patterns in monocot stems for systematic purposes.

The present study has shown that morphological and structural organization among all the Princeton monocotyledons had reached a level of evolutionary specialization comparable to that found in extant monocotyledons. As pointed out in this study, accurate systematic treatment of permineralized monocotyledons stresses the importance of detailed anatomical studies of all vegetative organs of extant monocots, especially studies that take into account the effects of age and environmental conditions on internal structure. Also, the reconstruction of whole fossil plants is particularly important with respect to their systematic treatment. Heleophyton is known only from a single petiole fragment; however, continued study of the chert should yield the vegetative body and reproductive parts necessary to fully reconstruct this plant. Likewise, discovery of the flowers, fruits, and seeds of Uhlia, Ethela, and Soleredera will permit a more refined systematic treatment of these plants thus providing a stronger data base on which to establish phylogentic relationships of these early Tertiary monocotyledons.

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